Grzimek's Animal Life Encyclopedia

Second Edition
Volumes 4 & 5 • Fishes I & II

Michael Hutchins, Series Editor,
in association with the American Zoo and Aquarium Association

Dennis A. Thoney and Paul V. Loiselle, Advisory Editors

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Animal Life Encyclopedia

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Volume 4
Fishes I

Dennis A. Thoney, Advisory Editor
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Joseph E. Trumpey, Chief Scientific Illustrator

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Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E.O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa-regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in super markets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"-places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade-the hunting of endangered wild animals for large scale human consumption-is pushing many species, including our closest relatives, the gorillas, bonobos and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought

specialists from various disciplines to write the sections with which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 205 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Grzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909–1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series has been completely revised and updated for the first time in over 30 years. Gale expanded the series from 13 to 17 volumes, commissioned new color paintings, and updated the information so as to make the set easier to use. The order of revisions is:

Volumes 8–11: Birds I–IV
Volume 6: Amphibians
Volume 7: Reptiles
Volumes 4–5: Fishes I–II
Volumes 12–16: Mammals I–V
Volume 3: Insects
Volume 2: Protostomes
Volume 1: Lower Metazoans and Lesser Deuterostomes
Volume 17: Cumulative Index

Organized by taxonomy

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science in which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the lower metazoans and lesser deuterostomes, in volume 1, the series progresses through the more advanced classes, culminating with the mammals in volumes 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. In the case of the volumes on Fishes, introductory chapters describe general characteristics of fishes, followed by taxonomic chapters dedicated to order and, in a few cases, suborder. Readers should note that in a few instances, taxonomic groups have been split among more than one chapter. For example, the order Cypriniformes is split among two chapters, each covering particular families. Species accounts appear at the end of the taxonomic chapters. To help the reader grasp the scientific arrangement, order and suborder chapters have distinctive symbols:

● = Order Chapter
○ = Suborder Chapter

The order Perciformes, which has the greatest number of species by far of any fishes order—and in fact is the largest order of vertebrates—has been split into separate chapters based on suborder. Some of these suborder chapters are again divided into multiple chapters in an attempt to showcase the diversity of species within the group. For instance, the suborder Percoidei has been split among four chapters. Readers should note that here, as elsewhere, the text does not necessarily discuss every single family within the group; in the case of Percoidei, there are more than 70 families. Instead, the text highlights the best-known and most significant families and species within the group. Readers can find the complete list of families for every order in the "Fishes family list" in the back of each Fishes volume.

As chapters narrow in focus, they become more tightly formatted. Introductory chapters have a loose structure, reminiscent of the first edition. Chapters on orders and suborders are more tightly structured, following a prescribed format of standard rubrics that make information easy to find. These taxonomic chapters typically include:

- Scientific name of order or suborder
- Common name of order or suborder
- Class
- Order
- Number of families

Main chapter
- Evolution and systematics
- Physical characteristics
- Distribution
- Habitat
- Feeding ecology and diet
- Behavior
- Reproductive biology
- Conservation status
- Significance to humans

Species accounts
- Common name
- Scientific name

Family
Taxonomy
Other common names
Physical characteristics
Distribution
Habitat
Feeding ecology and diet
Behavior
Reproductive biology
Conservation status
Significance to humans
Resources
Books
Periodicals
Organizations
Other

Color graphics enhance understanding

Grzimek's features approximately 3,500 color photos, including nearly 250 in the Fishes volumes; 3,500 total color maps, including more than 200 in the Fishes volumes; and approximately 5,500 total color illustrations, including nearly 700 in the Fishes volumes. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges.

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal specimens from the University of Michigan Zoological Museum library. In addition to illustrations of species, *Grzimek's* features drawings that illustrate characteristic traits and behaviors.

About the contributors

All of the chapters were written by ichthyologists who are specialists on specific subjects and/or families. The volumes' subject advisors, Dennis A. Thoney and Paul V. Loiselle, reviewed the completed chapters to insure consistency and accuracy.

Standards employed

In preparing the volumes on Fishes, the editors relied primarily on the taxonomic structure outlined in *Fishes of the World*, 3rd edition, by Joseph S. Nelson (1994), with some modifications suggested by expert contributors for certain taxonomic groups based on more recent data. Systematics is a dynamic discipline in that new species are being discovered continuously, and new techniques (e.g., DNA sequencing) frequently result in changes in the hypothesized evolutionary relationships among various organisms. Consequently, controversy often exists regarding classification of a particular animal or group of animals; such differences are mentioned in the text.

Grzimek's has been designed with ready reference in mind, and the editors have standardized information wherever feasible. For ***Conservation Status,*** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN web page at <http://www.iucn.org/themes/ssc/redlists/categor.htm>.

In addition to IUCN ratings, chapters may contain other conservation information, such as a species' inclusion on one of three Convention on International Trade in Endangered Species (CITES) appendices. Adopted in 1975, CITES is a global treaty whose focus is the protection of plant and animal species from unregulated international trade.

In the Species accounts throughout the volume, the editors have attempted to provide common names not only in English but also in French, German, Spanish, and local dialects. Readers can find additional information on fishes species on the Fishbase Web site: <http://www.fishbase.org>.

Grzimek's provides the following standard information on lineage in the ***Taxonomy*** rubric of each Species account: [First described as] *Acipenser brevirostrum* [by] LeSueur, [in] 1818, [based on a specimen from] Delaware River, United States. The person's name and date refer to earliest identification of a species, although the species name may have changed since first identification. However, the entity of fish is the same.

Readers should note that within chapters, species accounts are organized alphabetically by family name and then alphabetically by scientific name. In each chapter, the list of species to be highlighted was chosen by the contributor in consultation with the appropriate subject advisor: Dennis A. Thoney, who specializes in marine fishes; and Paul V. Loiselle, who specializes in freshwater fishes.

Anatomical illustrations

While the encyclopedia attempts to minimize scientific jargon, readers will encounter numerous technical terms related to anatomy and physiology throughout the volume. To assist readers in placing physiological terms in their proper context, we have created a number of detailed anatomical drawings. These can be found on pages 6 and 7, and 15–27 in the "Structure and function" chapter. Readers are urged to make heavy use of these drawings. In addition, selected terms are defined in the ***Glossary*** at the back of the book.

Appendices and index

In addition to the main text and the aforementioned ***Glossary,*** the volume contains numerous other elements. ***For Further Reading*** directs readers to additional sources of information about fishes. Valuable contact information for ***Organizations*** is also included in an appendix. An exhaustive ***Fishes family list*** records all recognized families of fishes according to *Fishes of the World*, 3rd edition, by Joseph S. Nelson (1994). And a full-color ***Geologic time scale*** helps readers understand prehistoric time periods. Additionally, the volume contains a ***Subject index.***

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Topic overviews

What is a fish?

Evolution and systematics

Structure and function

Life history and reproduction

Freshwater ecology

Marine ecology

Distribution and biogeography

Behavior

Fishes and humans

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What is a fish?

What is a fish?

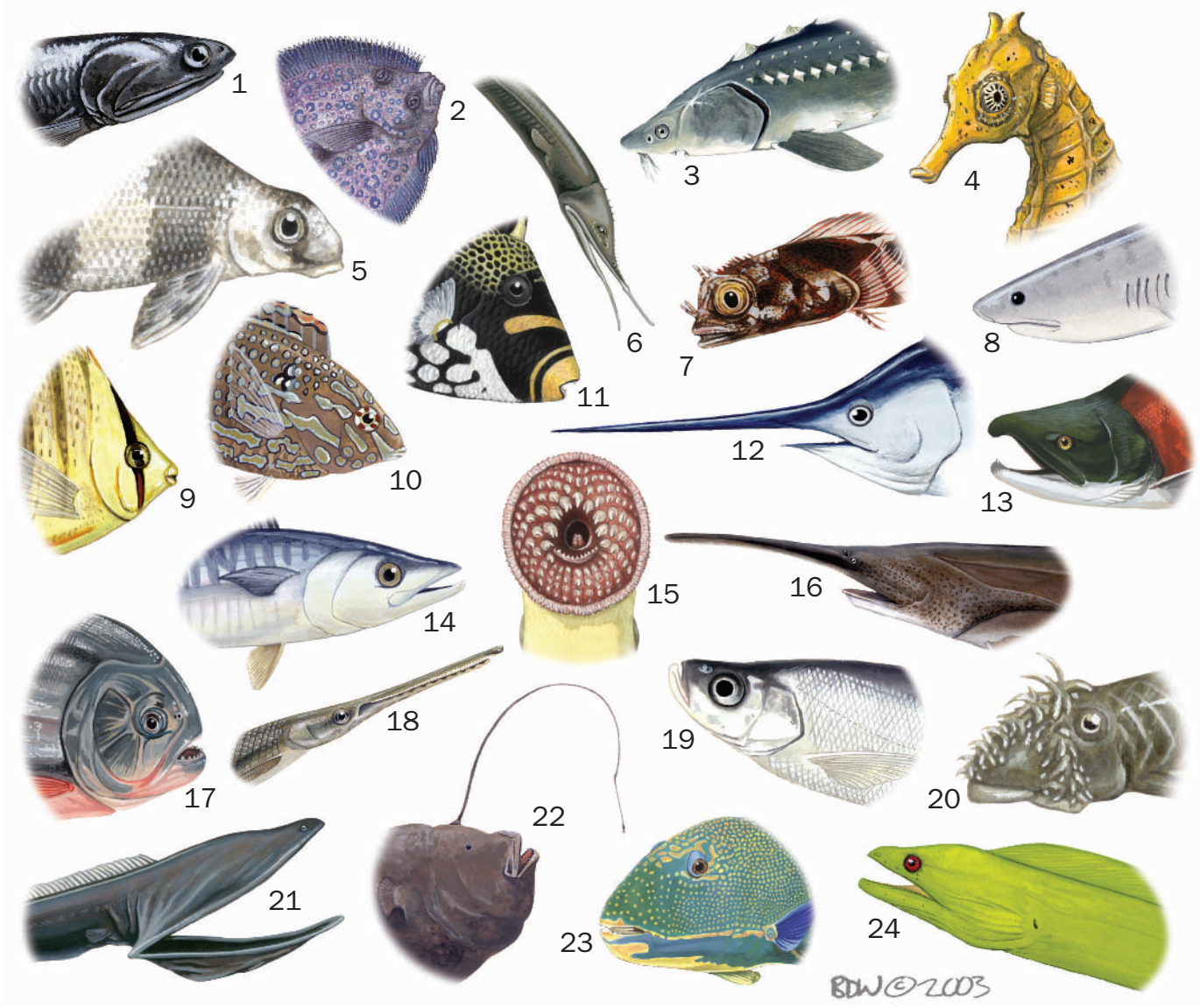
The concept of "fish" certainly is more steeped in tradition than backed by scientists, despite the fact that countless ichthyologists (i.e., scientists who study fish) have written innumerable pages on the subject. The reality that fishes in the broadest sense have long played important roles in the promotion of industry and commerce, geographic exploration, politics, art, religion, and myth mandates that the definition of fish can vary according to human perspective and sometimes despite science. For example, from a chef's point of view, fishes come in two basic varieties—shellfish and finfish. Scientists eschew such groupings of distantly related creatures. However, lest they be hoisted with their own petards, ichthyologists might tread gently on the many concepts of fish, for they must acknowledge science's inability to form an absolute taxonomic definition of "fish" based on biological characteristics that are shared by all fishes and yet not shared with any "nonfish."

A starry moray eel (*Gymnothorax nudivomer*) peering out from its home near the Philippines. (Photo by Robert Yin/Corbis. Reproduced by permission.)

This whale shark (*Rhincodon typus*) measures 40 ft (12 m). Whale sharks are the largest fish on the earth today. (Photo by Amos Nachoum/Corbis. Reproduced by permission.)

Defining characteristics

Widespread views of the particular characteristics that define fishes, of course, are biased by general familiarity with extant (i.e., living) species and, in particular, with the widespread and well-known bony fishes. Thus, the notion of a fish as an aquatic ectothermic vertebrate possessing gills, paired and unpaired fins, and scales usually suffices as a casual definition of fish. Reasonable as this definition may seem, some of these characteristics are shared with other groups of animals that are not considered fishes, while others of them are not common to all fishes. For example, although most fish live in water, some fishes, such as the walking catfish (*Clarias batrachus*) or African lungfish (*Protopterus* species) can spend considerable periods out of water. Furthermore, other fishes may spend much briefer, yet highly significant periods out of water, which allow them to feed (e.g., mudskippers, *Periophthalmus*



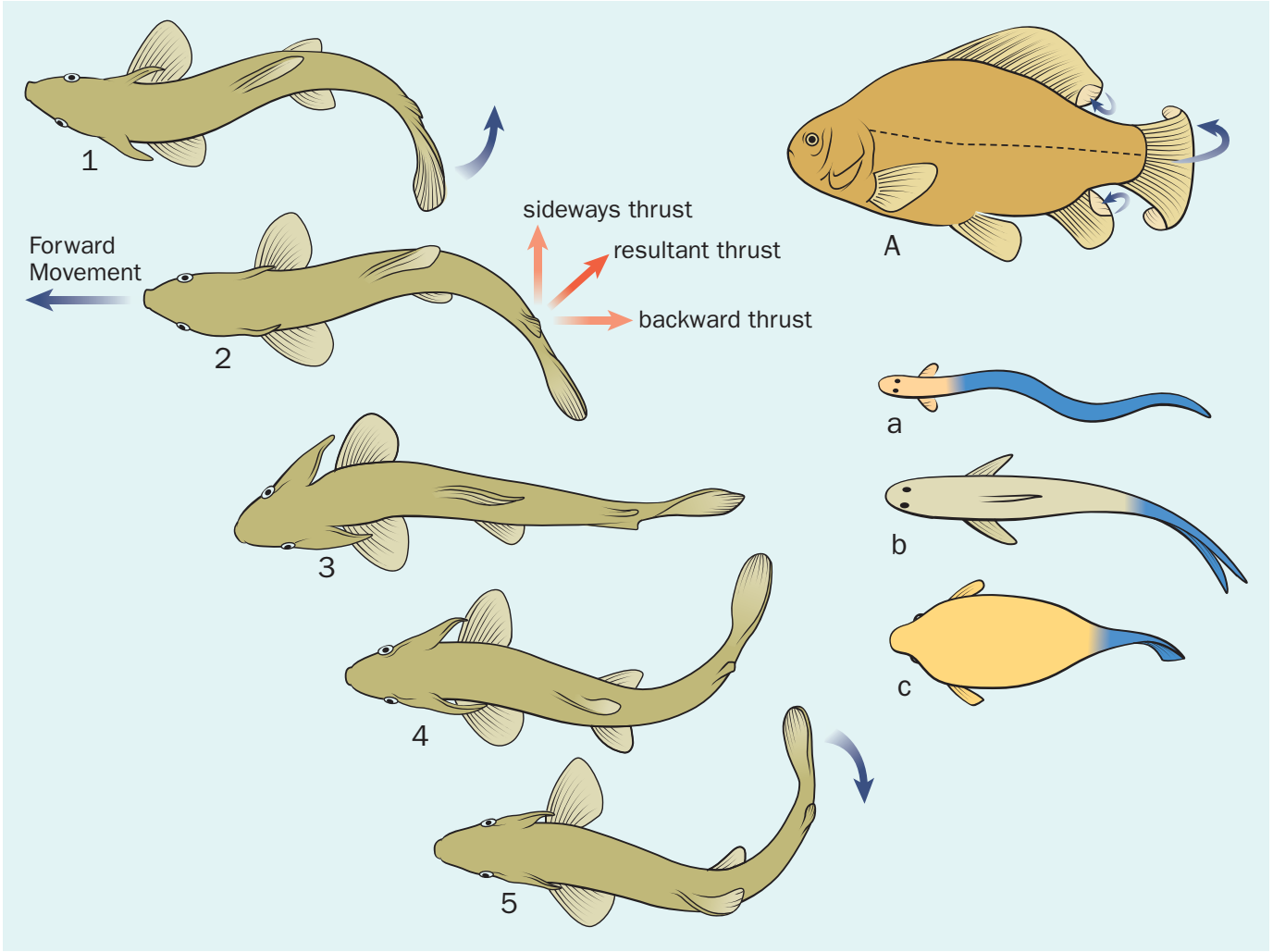
Mouth morphology comparison among fishes. 1. Northern anchovy (*Engraulis mordax*); 2. Peacock flounder (*Bothus lunatus*); 3. White sturgeon (*Acipenser transmontanus*); 4. Yellow seahorse (*Hippocampus kuda*); 5. Chinese sucker (*Myxocyprinus asiaticus*); 6. Bobtail snipe eel (*Cyema atrum*); 7. Secretary blenny (*Acanthemblemaria maria*); 8. Tiger shark (*Galeocerdo cuvier*); 9. Pebbled butterflyfish (*Chaetodon multicinctus*); 10. Blackspotted wrasse (*Macropharyngodon meleagris*); 11. Clown triggerfish (*Balistoides conspicillum*); 12. Swordfish (*Xiphias gladius*); 13. Sockeye salmon (*Oncorhynchus nerka*); 14. King mackerel (*Scomberomorus cavalla*); 15. Sea lamprey (*Petromyzon marinus*); 16. Paddlefish (*Polyodon spathula*); 17. Red-bellied piranha (*Pygocentrus nattereri*); 18. Longnose gar (*Lepisosteus osseus*); 19. Minnow (*Culter alburnus*); 20. Catfish (*Ancistrus triradiatus*); 21. Pelican eel (*Eurypharynx pelecanoides*); 22. Krøyer's deep sea anglerfish (*Ceratias holboelli*); 23. Bicolor parrotfish (*Cetoscarus bicolor*); 24. Green moray (*Gymnothorax funebris*). (Illustration by Bruce Worden)

spp., and the arowanas, *Osteoglossum* spp.) or flee from predators (e.g., flyingfishes, Exocoetidae).

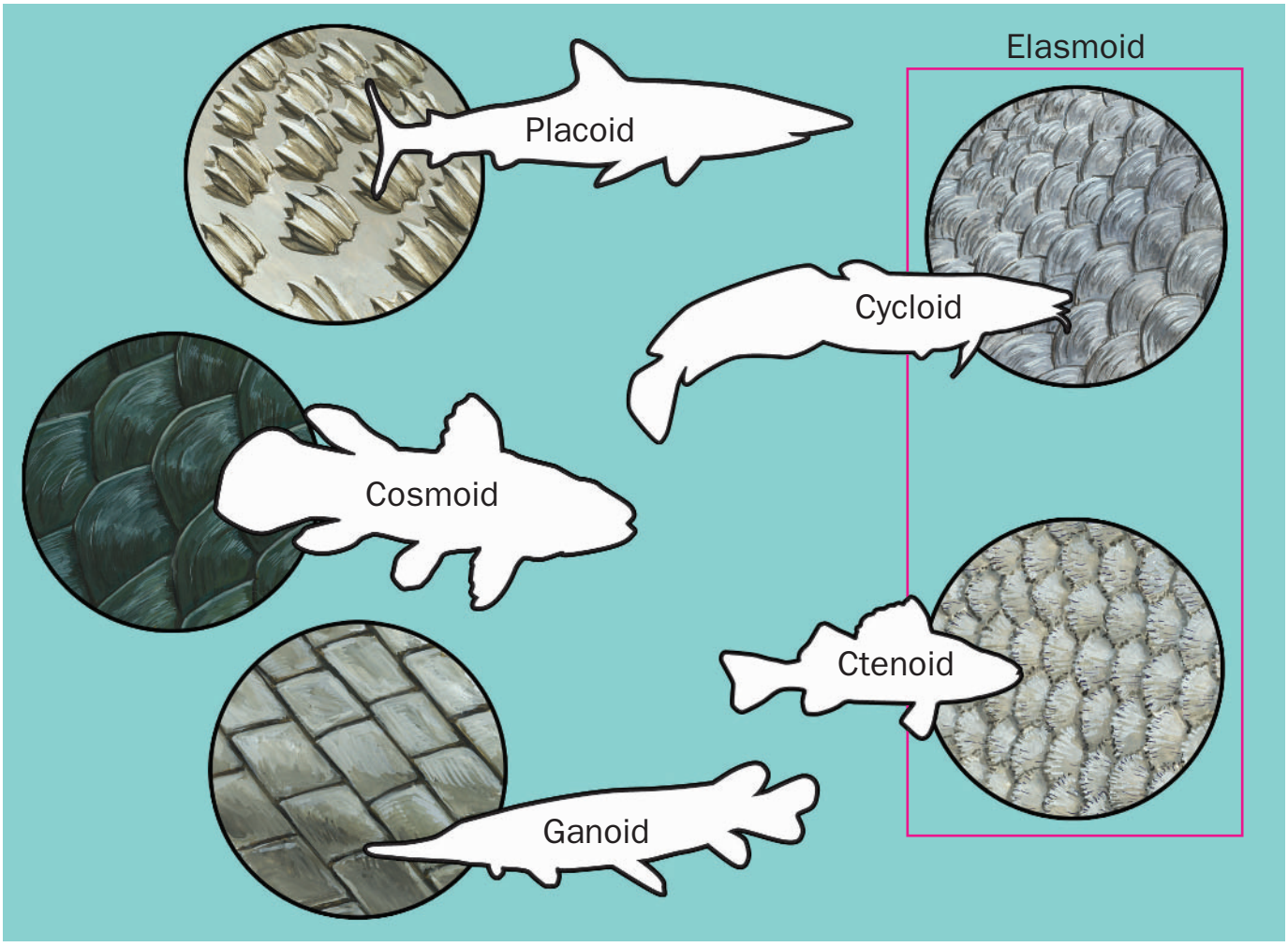
Similarly, whereas most fishes cannot control their body temperature other than through behavioral mechanisms involving migrations or local movements to and from waters of varying warmth, some lamnids (Lamnidae) and tunas (*Thunnus* spp.) and the swordfish (*Xiphias gladius*) can maintain body temperatures that are several degrees higher than the water that surrounds them for significant periods. Certainly, most fishes possess a well-developed vertebral column; however, hagfishes (Myxinidae) lack well-defined vertebrae, and there is disagreement among scientists regarding whether this characteristic exists because the ancestors of these fishes were similar or, antithetically, because vertebrae were "lost" from this lineage through evolutionary modification. In fact, so different are hagfishes from other fishes that Aristotle considered them members of another, illegitimate taxonomic group—worms. Unlike worms, fishes are chordates (phylum Chordata), and they possess skeletal components that form a cranium (i.e., a brain case). This characteristic (as well as many others) distinguishes them from some fishlike chordates, such

The Hawaiian anthias (*Pseudanthias ventralis*) is one of many fishes that has vibrant, incredible colors. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

A pike (*Esox lucius*) with a newly caught frog. (Photo by Animals Animals ©C. Milkins, OSF. Reproduced by permission.)



Fish use their tails to propel themselves through the water. A. A crucian carp's fin action for stabilizing and maneuvering. a. Anguilliform locomotion (eel); b. Carangiform locomotion (tuna); c. Ostraciform locomotion (boxfish). The blue area on these fish shows the portion of the body used in locomotion. (Illustration by Patricia Ferrer)



Scale types and patterns in fish. Clockwise from top: Placoid, cycloid, ctenoid, ganoid, cosmoid. (Illustration by Brian Cressman)

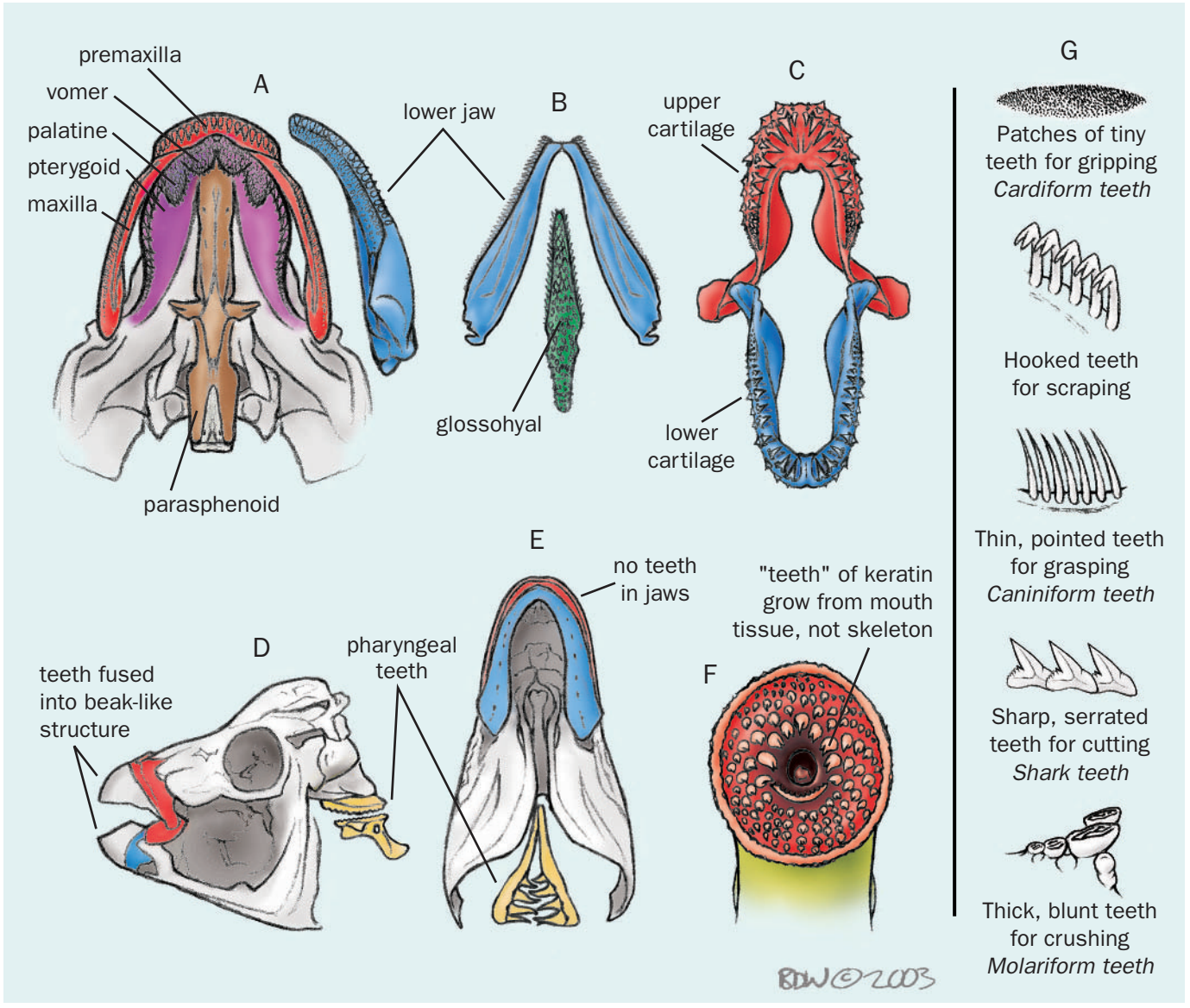
as the lancelets (Amphioxiformes), but, of course, amphibians, reptiles, birds, and mammals also have a cranium.

Gills cannot be used as an unequivocal characteristic defining fishes, because some amphibians have and use gills for at least a portion of their lives. Furthermore, whereas most fishes obtain oxygen from water through conventional gills, some fishes significantly supplement gill respiration by acquiring oxygen from the water or atmosphere via modified portions of the gills (e.g., the walking catfish) or skin (e.g., the European eel, *Anguilla anguilla*) or specialized tissues in the mouth (e.g., the North American mudsucker goby, *Gillichthys mirabilis*), gut (e.g., plecostomuses, *Plecostomus* species), swim bladder (e.g., the bowfin, *Amia calva*), or lungs (e.g., the Australian lungfish, *Neoceratodus forsteri*). Complicating matters still further, some fishes are obligate air breathers and must have access to the atmosphere or they will drown (e.g., the electric eel, *Electrophorus electricus* and the South American lungfish, *Lepidosiren paradoxa*).

At first glance, fins seem to define fishes. Several unrelated groups of nonfishes (e.g., lancelets, sea snakes, and some amphibians) possess finlike modifications associated with their tails that facilitate locomotion in water. Furthermore, although some fishes, such as hagfishes and lampreys (Petromyzontidae), lack paired fins, the paired appendages of amphibians, reptiles, birds, and mammals are considered homologous to the paired fins of fishes. Likewise, the scales that cover many common bony fishes are not a universally acceptable distinguishing feature, because numerous unrelated groups of fishes lack scales, for example, the hagfishes, the lampreys, and the North American freshwater catfishes (Ictaluridae). Moreover, those fishes that possess scales may be more or less covered by one of several basic scale types, for example, the placoid scales of sharks, the ganoid scales of gars, and the bony ridge scales of salmon and basses. These differences in the scales of fishes point to the fact that some other aquatic chordates, such as sea snakes, also have scales, even though the outer coverings of reptiles, birds, and mammals are heavily keratinized, whereas those of fishes are not.

Superclass Pisces as a polyphyletic group

Given that no one characteristic distinguishes all fishes from all other organisms, even the most committed ichthyologist must admit that the superclass Pisces (an assemblage that in-



Tooth morphology and tooth-bearing structures typical of fishes: A. Bowfin (*Amia calva*); B. Mooneye (*Hiodon tergisus*); C. Sand shark (*Odontaspis taurus*); D. Parrotfish (*Scarus guacamaia*); E. Northern pikeminnow (*Ptychocheilus oregonensis*); F. Sea lamprey (*Petromyzon marinus*); G. Tooth forms and functions. (Illustration by Bruce Worden)

cludes all fishes) represents an unnatural or polyphyletic group. In fact, given our scientific understanding of fishes as of 2002, the only measure allowing them to stand together as a natural or monophyletic group requires the inclusion of all other craniates (i.e., amphibians, reptiles, birds, and mammals). Most biologists probably would agree that the consideration of all craniates as fishes would be of little scientific value and would betray the longstanding and widespread conception of a fish. In light of this situation, uncompromising cladists returning from a fishing trip for salmon are condemned to telling others of having been "salmoning" rather than "fishing."

General definition of fish

Despite the seemingly hopeless conundrum of defining "fish" scientifically, many scientists and non-scientists probably would agree that a general definition for this loose group of animals can be established. For these reasonable folks, a fish can be defined as an ectothermic chordate that lives primarily in water and possesses a cranium, gills that are useful virtually throughout life, and appendages (if present) in the form of fins. Those not willing to endorse this definition might rest easy by considering "fish" as the raison d'être for ichthyologists.

Resources

Books

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Evolution and systematics

Origin of fishes

Fishes are the most primitive members of the subphylum Craniata. The subphylum was previously called Vertebrata, but Janvier (1981) demonstrated that the most primitive members of the taxon possess a cranium but lack arcualia, or rudimentary vertebral elements. Thus the taxon is better termed Craniata than Vertebrata. Vertebrata is reserved for a subset of Craniata that possesses vertebral elements, in addition to a cranium. Two recently discovered fossils from China (Shu et al, 1999) extend the fossil record of fishes back to the early Cambrian, 530 million years ago (mya). These early forms are either the direct ancestors or the indirect ancestors to nearly all of the vertebrates, and their discovery suggests that vertebrates were part of the great explosion of metazoan life in the Cambrian. The fossils are small, about 0.98 to 1.1 in (25 to 28 mm) long, and possess a cartilaginous cranium, five to nine gill pouches, a large heart located behind the last pair of gill pouches and possibly enclosed in a pericardium, a notochord, zigzag-shaped muscle blocks or myomeres, and a dorsal fin (one of the two forms) supported by fin rays or radials. The more generalized fossil, *Myllokunmingia*, is thought to be the sister group of craniates except for the hagfishes. The other fossil, *Haikouichthys*, is considered to be a close relative of the lampreys. Unlike most other jawless fishes, these early forms lacked scales or bony armor. Until near the end of the twentieth century, evidence of vertebrates in the Cambrian was inconclusive. Carapace fragments thought to represent Ostracoderms, a group of armored, jawless fishes abundant in the Ordovician to the Devonian, were present in the Cambrian, but other experts consider the fragments to represent the carapaces of arthropods. Isolated, tooth-like elements, or conodonts, were common in the fossil record, but these elements could not be assigned to an organism. In the mid-1980s conodonts were discovered to be specialized feeding elements of soft-bodied, eel-like fossils possessing a notochord, dorsal nerve cord, V-shaped myomeres, and large eyes. Conodonts are considered to be the sister group of the remainder of vertebrates other than lampreys.

Other recent discoveries illustrate that craniates and vertebrates were rather diverse by the middle Ordovician (450 mya) (Young 1997, Sansom et al. 1996), with both jawless and jawed forms represented. Despite the occurrence of jawed fishes in the Ordovician, jawless forms dominated until the late Silurian. Ostracoderms are classified into about 10 to 12 major groups with poorly resolved relationships (Janvier 1999). However, it appears that this group is the sister group of the jawed fishes (gnathostomes). Most of the fossils representing these taxa possessed mineralized exoskeletons (except for the *Jamoytius*, and possibly *Euphanerops*), head shields (except for Anaspida, *Endeiolepis*, and Thelodonti) and multiple gill openings (except in Heterostraci), and lacked paired fins (except for the Anaspida, Osteostraci, Pituriaspida, and Thelodonti).

Modern jawless fishes

Myxiniformes (hagfishes) and Petromyzontiformes (lampreys) are modern jawless fishes that first appear in the Pennsylvanian (300 mya) and the late Mississippian (330 mya), respectively. Based on the structure of their pouch-like gills and several other characteristics, the two taxa were previously thought to form a monophyletic group, but as of 2002 they are considered to be paraphyletic, in that they do not share a common ancestor. Hagfishes are hypothesized to be the sister group to the remainder of the vertebrates. They are slender bodied and naked, lack fins with exception of the caudal fin, have degenerate eyes, four pairs of tentacles around the mouth and nasal openings, an esophago-cutaneous duct leading from the exterior to the esophagus, one semicircular canal in the inner ear, gill pouches posterior to the head, and ventrolateral slime glands. They are additionally distinguished from the vertebrates in lacking vertebral elements. Modern hagfishes are limited to soft bottom marine habitats and feed on soft-bodied, burrowing invertebrates and carrion. Lampreys are considered to be the next branch of the craniate tree and are slender bodied and naked, have two dorsal fins, a sucker surrounding the mouth, a rasping and sucker device (termed a tongue) that can be protruded from the mouth, two semicircular canals in the inner ear, and a dorsally located nasohypophysial opening on the head. Lampreys occur in fresh and marine waters, and some are anadromous, spending most of their adult lives in salt water and then migrating to freshwater streams and rivers to reproduce. Larvae are fossorial, or live in soft bottoms and filter feed on algae and detritus. Adults either are ectoparasites on ray-finned fishes or do not feed after metamorphosis from the larval to the adult stage. According to this phylogenetic scenario, the lack of a bony

A side-by-side view of a contemporary white shark tooth (left) and a megalodon tooth. The megalodon was a prehistoric great white shark. (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

skeleton and scales in hagfishes and lampreys is primitive rather than a specialization related to their fossorial or parasitic life styles.

Origin of jawed fishes

Jawed fishes, Gnathostomata, possess true mandibular jaws, paired fins, inner ears with three semicircular canals, and gill arches internal to ectodermal gill filaments. Gnathostomes date back to the Ordovician (450 mya) but did not dominate aquatic regions of the world until the mid-to-late Devonian. Thus, jawless and jawed fishes coexisted for about 100 million years. The earliest jawed fish fossils are chondrichthyans, one of the five major groups of gnathostomes. Chondrichthyans today are represented by the chimaeras, sharks, skates, and rays, and are distinguished from the other four groups in lacking dermal bone, possessing cartilaginous rather than bony endoskeletons, and having distinctive gill filaments, multiple gill openings (except for the chimaeroids), horny unsegmented fin rays (ceratotrichia), and embryos encapsulated in leathery capsules. The Placodermi, likely the sister group of the chondrichthyans, appear in the early Silurian (420 mya). They assumed a wide variety of body forms and dominated fresh and salt waters in the Devonian before their extinction by the Mississippian. Some, such as Rhenaniformes and Ptyctodontiformes, were very similar in structure to modern chondrichthyans, such as rays and chimaeroids. Placoderms had bony head and shoulder plates, with the head shield movably articulating with the trunk shield, but lacked true teeth. Acanthodii first appeared in the early Silurian, reached peak diversity in the Devonian, and apparently became extinct in the Permian. They were small, slender, and elongate fishes that possessed dermal or endochondral bone, bony covering over gill slits, stout spines preceding fins, and scales covering most of the body. Some forms may have possessed endochondral bone, but most apparently had cartilaginous endoskeletons. The last two groups of fishes, the Actinopterygii and Sarcopterygii, together comprise the Osteichthyes, and are thought to be the sister group of the acanthodians. The Osteichthyes have bony endoskeletons (endochondral bone) and lungs or swim bladders. The actinopterygians first appear in the late Silurian (410 mya) and today constitute the great majority of fishes. This group is distinguished by possessing ganoid or elasmoid scales, pectoral fin radials directly connected to scapulocoracoid or shoulder girdle, and nostrils located high on the head. Sarcopterygii are known from the Devonian (400 mya). They are distinguished in possessing true tooth enamel, reduction of branchial skeleton, and presence of a pulmonary vein. The reduced branchial skeleton and pulmonary vein suggest that they relied, at least in part on aerial respiration.

Chondrichthyans

Although fossil evidence in the form of scales has pushed the origin of chondrichthyans back to the Ordovician, cartilaginous fishes do not become abundant in the fossil record until the Carboniferous period. Throughout their history chondrichthyans have undergone several major radiations but today display only a modest radiation in body shape and are represented by a relatively small number of species. The Paleozoic cartilaginous fishes resemble recent forms but generally had terminal jaws, lacked vertebral centra, had fin radials that extended to the fin margins, and lacked skeletal connections between the halves of their pectoral and pelvic girdles. All but the earliest taxon, *Cladoselache* possessed male intromittent organs, suggesting that like their modern counterparts, they practiced internal fertilization and development. In the early Carboniferous, elasmobranchs underwent their second radiation. Male stethacanthid sharks, present from the late Devonian to the Permian, had bony, brush-like structures along the margin of the dorsal fin or modified dorsal fin spines bearing denticles, tooth-like scales (or placoid scales) that form distinctive patterns on the skin of various species of sharks. Some edestoid sharks had complex, coiled tooth whorls extending from their lower jaws that functioned in some unknown manner. Holocephalans, distinguished by possessing gill covers, upper jaw fused to the cranium, and crushing dentition, were described from the Upper Devonian and assumed a wide variety of forms in the Carboniferous, some resembling modern ray-finned fishes. Chondrichthyans suffered large number of extinctions at the end of the Permian, as did much of the world's biota, as the result of either extensive volcanic activity or a large asteroid's striking Earth. The final radiation of chondrichthyans began in the Jurassic, evolving from a lineage that survived the end of the Paleozoic extinction event(s). Nearly all modern families are represented in the fossil record by the end of the Mesozoic. Modern chondrichthyans generally possess subterminal jaws, vertebral centra, fin radials that fall short of the fin margins, and cartilaginous connections between the halves of their pectoral and pelvic girdles.

The recent chondrichthyans consist of two natural groups, the Holocephali, or chimaeroids, and the Neoselachii, or sharks and rays. In total, there are about 900 to 1000 living chondrichthyans. The chimaeroids number about 45 species and resemble some of their more conservative Carboniferous relatives. Anatomical research in the 1980s and 1990s con-

cluded that the Neoselachii consisted of two basal groups, the Galeomorphii and Squalea, distinguished by a number of technical aspects of their skeletal structure and musculature. In this scenario the rays (Rajiformes) made up a terminal node of the Squalea. Molecular studies, however, suggest that sharks and rays are sister groups that in turn are the sister group of the chimaeroids. The division of sharks into Galeomorphii and Squalea is supported by the molecular studies.

The galeomorphs consist of four orders: Heterodontiformes (horn sharks), Orectolobiformes (wobbegons, nurse sharks, whale sharks), Lamniformes (sand tigers, basking sharks, thresher sharks, mackerel sharks), and Carcharhiniformes (catsharks, hound sharks, requiem sharks, and hammerheads). These sharks vary from benthic to pelagic and are best represented in tropical to warm, temperate seas. The Squalea consist of four major groups: Hexanchiformes (frill sharks, cowsharks), Squaliformes (sleeper sharks, dogfish sharks), Squatiniformes (angelsharks), and Pristiophoriformes (sawsharks). For the most part, these squalean sharks are associated with sea bottoms, often in deep water, and in temperate to boreal seas, although the Squatiniformes and Pristiophoriformes are exceptions in being distributed in tropical to warm temperate seas.

The rays differ from the sharks in being depressed to various degrees and having the pectoral fins attached to the cranium rather than free of the cranium, gills located on the ventral side of the body rather than laterally, and anterior trunk vertebrae fused into a tube (synarchial) rather than lacking a synarchial. Rays include the Torpedinoidei (electric rays), Pristoidei (sawfishes); Rhinidae, Rhinobatidae, Platyrhinidae (guitarfishes); Rajidae (skates); and Myliobatoidei (stingrays). Rays are, for the most part, associated with the sea bottoms in shallow to deep water.

Actinopterygians

Unlike the chondrichthyans, the ray-finned fishes have undergone significant morphological evolution since their first appearance in the Silurian. The earliest forms, in many respects, resembled the early chondrichthyans in possessing a heterocercal tail, having pectoral fins inserting low on the flank, and pelvic fins inserting behind the pectoral fins on the lower abdominal region. Unlike the early sharks, they possessed a single dorsal fin, endochondral bone, scales that grew throughout the life of the individual, and segmented and paired fin rays (lepidotrichia) rather than ceratotrichia. The scales had peg and socket articulations and consisted of a ganoine exterior, dentinous layer, and a basal spongy bone. The jaw teeth were set in sockets of the dermal jaw bones, the upper jaw was fused with the dermal bones covering the head, and the jaws were obliquely suspended to the cranium by the palatoquadrate bone. These primitive fishes are represented by several relic fishes today: Polypteridae (bichirs), Acipenseridae (sturgeons), and Polyodontidae (paddlefishes). The latter two groups, however, are highly modified from their Devonian ancestors.

By the end of the Paleozoic, numerous taxa of ray-finned fishes, classified as Neopterygii, appear in the fossil record.

Fossil of the primitive fish *Osteolepis macrolepidotys*, from the Middle Devonian period, around 30 million years ago. This specimen was found in Old Red Sandstone in the Sandwick fish beds at Quoyloo, Orkney, Scotland. (Photo by Sinclair Stammers/Science Photo Library/Photo Researchers, Inc. Reproduced by permission.)

Neopterygii differ in a number of respects from the earlier forms. The upper jaw is partially freed from the cheek bones, the jaws are perpendicularly suspended from the cranium, the number of fin rays are reduced to equal the number of supporting bones, and for the most part, ganoid scales are replaced by thin, elasmoid membranous scales. The elements of the upper jaw are fused medially. Branchial bones supporting the gill filaments develop pharyngeal teeth that assist in processing food. Today the basal neopterygians are represented by Lepisosteidae (gars) and Amiidae (bowfins). Gars have specialized jaws, but both they and the bowfin retain many primitive structures of the early neopterygians (upper jaw partially attached to dermal head bones, heterocercal or abbreviated heterocercal caudal fins, and lungs rather than swim bladders).

Teleostei, ray-finned fishes with an externally symmetrical or homocercal caudal fin and upper dermal jaw bones free of other dermal head bones, arose from a neopterygian ancestor in the mid-to-late Triassic (220–200 mya). There are a large number of fossil Triassic and Cretaceous teleosts, many with uncertain phylogenetic relationships, and four modern lineages of teleosts: Osteoglossomorpha, Elopomorpha, Clupeomorpha, and Euteleostei. The osteoglossomorphs are distinguished in that the primary jaw teeth are located on the parasphenoid bone along the middle of the roof of the mouth and on the tongue. In addition, the caudal fin skeleton is very specialized. The taxon includes Osteoglossidae (bony tongues), Hiodontids (mooneyes), Notopteridae (featherfin knifefishes), and Mormyridae (elephantfishes). All species are limited to freshwaters and most are tropical in distribution. The elopomorphs are distinguished by possessing ribbon-like leptocephalus larvae and numerous branchiostegal rays uniting the hyoid (second gill arch) with the opercular bones. The group includes Elopiformes (ladyfishes and tarpons), Albuliformes (bonefishes), Anguilliformes (eels), and Saccopharyngiformes (gulper eels). Nearly all of the elopomorphs are marine fishes and range from shallow to deepwater and from benthic to pelagic. The clupeomorphs are

distinguished by their otophysic connection between extensions of the swimbladder and the inner ear within the cranium. The taxon includes the Ostariophysi (minnows, tetras, catfishes, and gymnotid eels) and the Clupeiformes (herring and anchovies). Ostariophysians dominate the freshwaters of the world. Clupeiforms range from marine to freshwater; the great majority are pelagic and consume plankton.

About half of living fishes are classified in Acanthopterygii that arose from an euteleostean ancestor in the Triassic or early Cretaceous. Because of the large number of taxa and vast morphological variation, the taxon is not well defined. Acanthopterygii are distinguished, in part, by having the pharyngeal teeth confined to the anterior gill arches, the swallowing muscle (retractor dorsalis) inserting on the upper segment of the third gill arch, and the ligament supporting the pectoral girdle attaching to the base of the cranium. Acanthopterygians comprise three major taxa: Mugilomorpha, Atherinomorpha, and Percomorpha. The mugilomorphs include the mullets, largely pelagic fishes found in shallow fresh and marine waters. Atherinomorphs include Atheriniformes (rainbowfishes and silversides), Beloniformes (needlefishes, sauries, halfbeaks, and flyingfishes), and Cyprinodontiformes (rivulines, killifishes, poeciliids, and pupfishes) and are surface swimming fishes found in both fresh and marine waters. The percomorphs comprise nine orders, 229 families, 2,144 genera, and over 12,000 species that dominate coastal marine waters, including coral reefs, but that are also well represented in most other aquatic habitats.

Sarcopterygii

Sarcopterygii, lobe-finned fishes, are the line of fishes that gave rise to the tetrapods (amphibians, reptiles, birds, and mammals), and the fishes of this lineage are better represented in the fossil record than in modern aquatic habitats. Sarcopterygians include Coelacanthimorpha (coelacanths), Porolepimorpha (including the Dipnoi or lungfishes), and Osteolepimorpha (rhipidistians). Coelacanths are well represented in the fossil record from the Devonian to the Upper Cretaceous, and two species are known in modern times. The taxon is distinguished by having a hinged cranium, possessing a three-lobed caudal fin, and lacking internal nares. Porolepimorpha first appear in the lower Devonian and are widespread in the fossil record until the end of the Carboniferous Period. The group, which includes the Dipnoi, is distinguished by either having slight mobility between the anterior and posterior sections of the cranium or by lacking mobility within the cranium, and in lacking true choanae or internal nares. Today Dipnoi are represented by six species in three families in freshwaters of Australia, South America, and Africa. Rhipidistians occur from the middle Devonian to the Lower Permian in the fossil record and are distinguished by possessing a hinged cranium, internal nares, and either a heterocercal or diphycercal caudal fin (fin equally developed above and below distal extension of body axis). Like some of their close sarcopterygian relatives, rhipidistians possessed pectoral fin bones that are homologues of the humerus, ulna, and radius of tetrapods.

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Organizations

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John D McEachran, PhD

Structure and function

Introduction

Fishes are phenomenally diverse in their anatomical and physiological characteristics. They have evolved spectacular and myriad anatomical and functional specializations to accomplish basic biological functions, such as feeding, moving, and reproducing. Through this diversity in structure and function, fishes have adapted to live successfully in a wide range of aquatic environments.

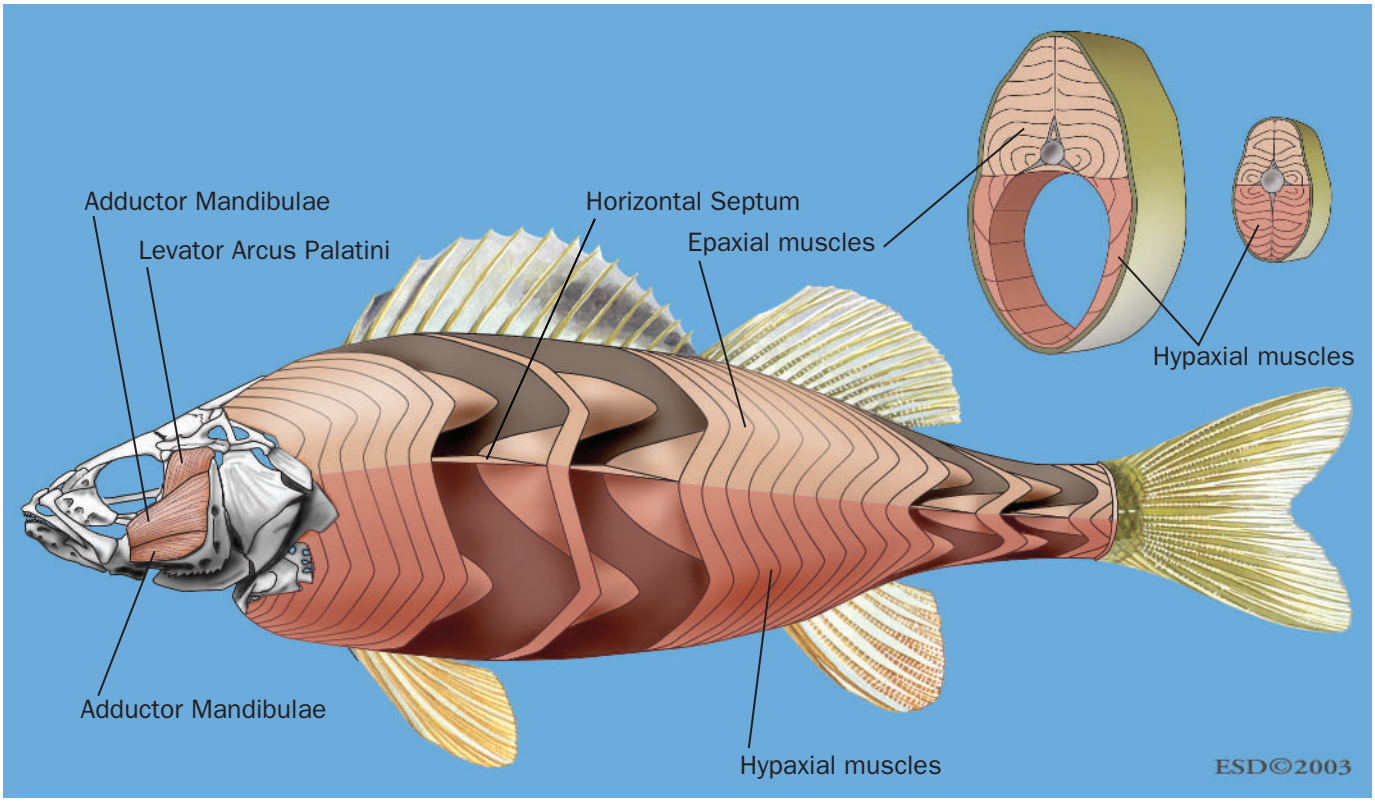
Body shape and external morphological features

Fishes vary in size by several orders of magnitude. The larval stages of many species are very small, many only a few millimeters in length. The largest fish species, the whale shark (*Rhincodon typus*), may reach a length of more than 59 ft (18 m). There is diversity in body shape as well, including elongate eels, fusiform tunas, dorsoventrally compressed fishes (such as skates and rays), and laterally compressed fishes (including flatfishes and many carangids). Body shapes are fascinating for their functional ingenuity. The flatfishes can lie against the bottom of the ocean, avoiding predators while being able to strike quickly at unsuspecting prey. The bullet-shaped bodies of tunas minimize water resistance for these high-performance cruising swimmers. Numerous unusual fish species have body shapes that make us wonder whether they are fish at all. Seahorses (genus *Hippocampus*), with their tapering prehensile tails and often spiky body armor, or related species, such as the leafy seadragon (*Phycodurus eques*), with leaflike projections from its fins and body surface, are camouflaged to blend in with the vegetation in which they live.

Fishes have many forms of locomotion that often correlate with external morphological features. The primarily axial movement patterns are classified into several swimming behaviors associated with backbone bending, including anguilliform, carangiform, and thunniform locomotion. Anguilliform movements, named after the eel genus *Anguilla*, typically are found in highly elongate species and involve axial bending along the entire axis of the fish. Carangiform movements, named after the family Carangidae (the jacks), entail more shallow body bends, with little bending near the head. Thunniform locomotion, named after the tuna genus *Thunnus*, involves movement of only the caudal backbone and caudal fin. Thunniform swimmers have many adaptations for efficient swimming, such as fins that can be tucked into grooves on the body to minimize drag, a narrow and stiff caudal peduncle (the area just anterior to the caudal fin), and a crescent-shaped caudal fin. The latter morphological feature minimizes drag on the tail while generating strong propulsive forces.

Fin shape strongly affects the shape and function of a fish's external form as well as its locomotor ability. Fishes have two sets of paired fins, the pectoral fins and pelvic fins, and several fins on the body midline, including one or more dorsal fins on the dorsal midline, a posterior caudal fin, and an anal fin on the ventral midline. Many fishes swim primarily with fin movements rather than with waves of axial bending. Ostraciiform locomotion (named for the family Ostraciidae, or boxfishes) involves movement of the caudal fin without axial bending. Amiiform locomotion, named for the basal actinopterygian fish *Amia calva*, or bowfin, consists primarily of waves of oscillation of a long dorsal fin. In contrast, gymnotiform locomotion (named for the family Gymnotidae, or knifefishes) comprises similar oscillations along an elongate anal fin. Many fishes, including the triggerfishes (family Balistidae) and pufferfishes (family Tetraodontidae), coordinate movements of the dorsal and anal fins. The pectoral fins are diverse in their morphological features and their function in locomotion. In swimming, most fishes use pectoral fins to turn and maneuver. The coral reef fish family Labridae and its relatives mainly use pectoral fin locomotion, and thus this type of swimming has been named labriform swimming. Some labriform swimmers literally fly underwater with a graceful up-and-down flapping motion, leaving their bodies straight as they dart around the reef.

Fins perform many functions other than locomotion, among them, feeding, defense, camouflage, breeding, and social display. Many species, such as the lumpfish (*Cyclopterus lumpus*), have pelvic fins modified as suction disks to prevent detachment from the substrate. Fins also are used for feeding, or to deter predation, in a variety of ways. Sea robins (family Triglidae) use sensory cells on the pectoral fins to find marine invertebrates buried in sediment on the ocean floor. Anglerfishes (order Lophiiformes) are named for the structure of the first dorsal spine, which has been modified into a fishing pole and bait, called, respectively, the illicium and the esca, held over the anglerfish's mouth. With this complex



Musculature of the yellow perch (*Perca flavescens*). Axial muscles are organized into nested cones that extend across several vertebral segments. At the lateral midline they are divided by the horizontal septum into epaxial (dorsal) and hypaxial (ventral) regions. The jaw muscles include the large adductor mandibulae and the levator arcus palatini muscles in the cheek region. (Illustration by Emily Damstra)

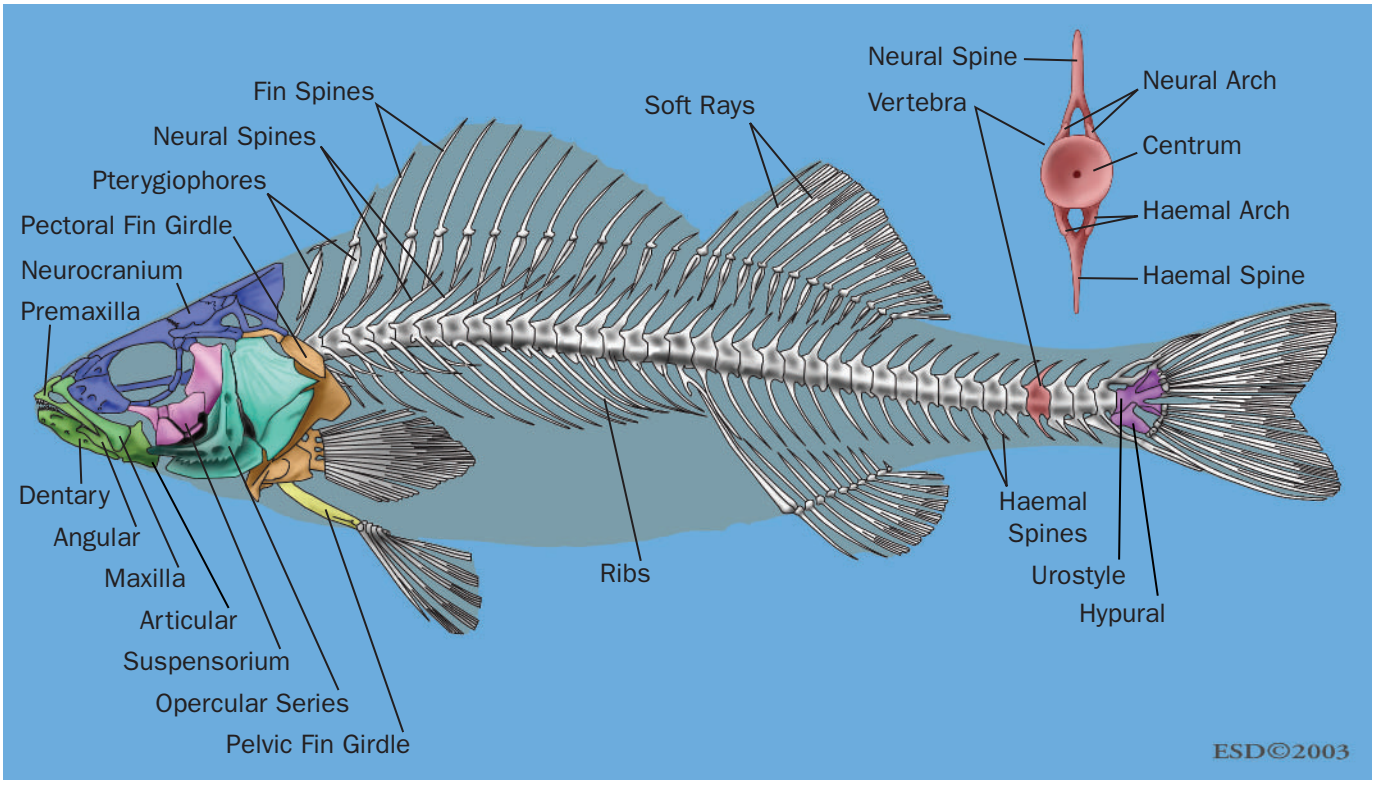
modified fin structure, they lure potential prey fish within range of easy capture. Other fin adaptations are meant to deter predators. As many fishermen have experienced, fin spines of even small fishes, such as sunfish (genus *Lepomis*), can be painfully sharp.

Fin spines also may be associated with unpalatable or noxious toxins that deter predators. Many members of the scorpionfishes (family Scorpaenidae) and related groups have sharp and toxic spines that they use as defense. The stonefish (genus *Synanceia*) has strong neurotoxins in its dorsal spines that can be injected into predators. Fins are used in reproductive behavior as well. In sharks and other elasmobranches (sharks, skates, and rays), intromittent organs called claspers have evolved from the pelvic fins. Similarly, the live-bearing fishes (family Poeciliidae) and related groups have modified anal fins that function as an intromittent organ called the gonapodium.

The integument

The body's covering, the skin and scales, provides a protective barrier to the external environment. As in other vertebrates, the skin of fishes has a deep dermal layer and a superficial epidermis. In fishes, glands in the epidermis secrete mucus that coats and protects the surface of the animal. Scales are formed from the dermal and epidermal layers of the skin. Chondrichthyans have placoid scales that are homologous to vertebrate teeth. At the base of each scale there is vasculature (blood vessels) covered with a dentine layer that is surrounded by enamel. Placoid scales are not replaced, but they increase in number with the growth of the fish. In some fish, such as the spiny dogfish (genus *Squalus*), placoid scales have been modified into large spines. The Osteichthyan fishes have several different scale types. Ganoid scales are found in basal groups of ray-finned fishes; they are formed from bony plates covered with a layer of ganoine and often create an interconnected armor over the surface of the body, as in bichirs (family Polypteridae) and gars (family Lepisosteidae). The scales of teleosts are derived from ganoid scales, losing the layer of ganoine to leave a thin plate of bone. Teleost scales are classified as ctenoid (toothed) and cycloid (circular) based on the shape of the outer edge. Unlike most placoid or ganoid scales, cycloid or ctenoid scales are arranged so as to overlap their more caudal neighbors. Scales protect the skin and deeper tissues from the environment. In many cases, as with ganoid scales, they form a tough armor against predators. Cycloid or ctenoid scales offer some protection from predators while not burdening the fish with the weight of heavy armor.

There is an amazing diversity in skin color patterns and their functions among fishes. Whereas some fishes use cryptic coloration to blend into their environments, others use bright colors or distinctive patterns to communicate. Cleaner fishes that pick parasites off other fish have bright colors and distinctive patterns that are recognizable by other species. Often color pattern is used to confuse or ward off predators. Toxic



Lateral view of the skeleton of the yellow perch (*Perca flavescens*). The principal tooth-bearing jaw elements are the dentary and premaxilla. The dentary, angular, and articular bones together form the lower jaw while the premaxilla and maxilla form the upper jaw. The jaws are connected to the neurocranium, the region of the skull surrounding the brain, by a series of bones that together are called the suspensorium. The opercular series, caudal and ventral to the suspensorium, covers the gills. The axial skeleton consists of a series of vertebrae. Each vertebra is composed of a centrum, neural spine, and arch, through which the spinal cord runs, and hemal spine and arch, through which passes the dorsal aorta. At the caudal end of the vertebral column the urostyle and mondified hemal spines called hypural bones support the muscles of the caudal fin. Other median fins are supported by pterygiophores that extend toward the vertebrae from the fins. The paired pectoral and pelvic fins are supported by the fin girdles. The bones of the pectoral fin suspend the fins from the neurocranium and support the fin rays and muscles. The pelvic girdle is not attached to the skull or vertebrae and its position varies among species. Soft rays and fin spines project from the base of the fins to support the fin membranes. (Illustration by Emily Damstra)

lionfishes (genus *Pterois*) have distinctive red and white stripes that warn potential predators. Eyespots on the caudal fin of many species may confuse predators about a fish's orientation.

Internal morphological features

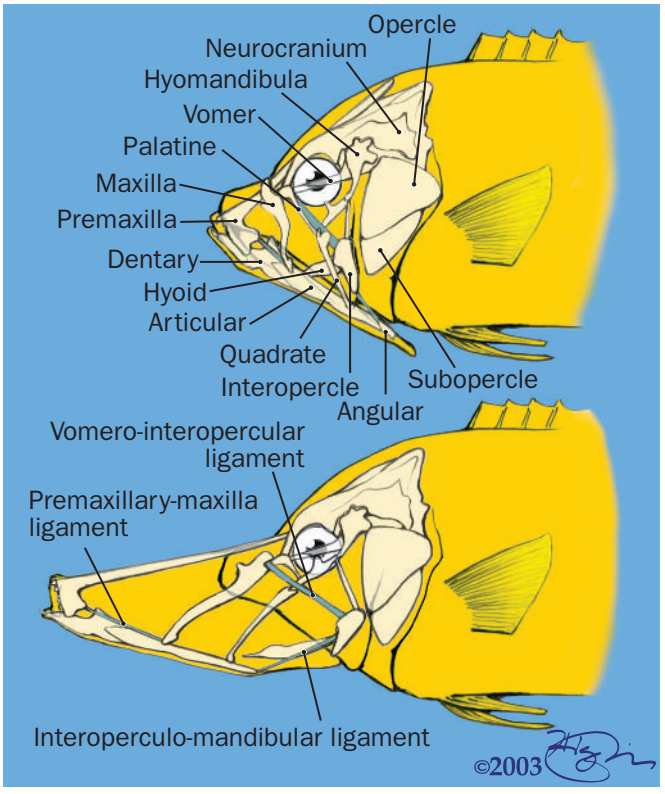
Cranial features and feeding

Unlike mammals, which have highly fused skulls with articulation only at attachments to the lower jaw and vertebral column, the cranium of fishes has more than 40 independently movable bony elements. These allow jaw protrusion, lateral expansion of the jaws, depression of the branchiohyoid apparatus and floor of the mouth, and movement of the gills and the operculum, which covers the gills. These movable elements are anchored to the neurocranium, which surrounds the brain and articulates with the vertebrae. The neurocranium corresponds to the chondrocranium, retained in chondrichthyan fishes, and additional dermal bones (the dermatocranium). As in other vertebrates, the neurocranium results from the fusion of many bones during development. The primary purpose of the neurocranium is to protect and support the brain. In addition, many species have a bone called the vomer, which forms part of the lower surface of the neurocranium, bears teeth, and aids in feeding.

The structure and function of fish jaws are astonishingly diverse, reflecting a wide array of feeding strategies and prey types that fishes exploit for food. This diversity results in large part from the increased mobility in the lower and upper jaws as well as the ability of fishes to incorporate other parts of their cranial anatomy into the feeding apparatus. In fishes both the upper and lower jaws articulate with the rest of the cranial skeleton, of which many elements are mobile. In bony fishes the primary jaws include the tooth-bearing premaxilla and, in more basal groups, maxilla in the upper jaw and the tooth-bearing dentary and the articular in the lower jaw. Dorsally, the premaxilla slides along the rostral end of the neurocranium. The upper and lower jaws connect caudally with each other and with the suspensorium, a group of bones suspended from the neurocranium. In addition, the lower jaw is connected to the series of opercular bones that covers the gills and to the hyoid apparatus in the floor of the mouth.

Several sets of bones form the floor of the mouth and wrap around the buccal cavity to connect to other cranial elements. The most rostral is the hyoid arch, involved in expansion of the buccal cavity. Following the hyoid arch are the branchial arches, which hold the gill structures, and, most caudally, the pharyngeal jaws, which bear teeth and help the fish eat prey. During feeding, jaw-depressor muscles rotate the lower jaw ventrally, causing the jaws to protrude forward. Suction forces are generated in the buccal cavity by dropping the floor of the mouth and flaring the suspensorium. The opercular bones seal the opercular opening to the gills. This combination of movements simultaneously leads to jaw protrusion, suction of water, and movement of the prey into the mouth.

The functional organization of jaw morphological features for feeding is a trade-off between the velocity of the movement and the force exerted. A striking example of a high-velocity feeding event involving extremely mobile jaws is illustrated by the slingjaw wrasse (*Epibulus insidiator*), aptly named for its ability to sling its jaws away from the rest of its head during the capture of evasive prey. This mechanism allows the rest of the body to remain still, minimizing the chances of being detected by the prey. An alternative strategy is seen in fishes that eat hard prey, such as mollusks, including the sheepshead (*Archosargus*). These fish do not feed on evasive prey, and so they do not need high-velocity jaw movements; instead, they maximize the force for crushing shells. The difference in feeding strategy is reflected in the lengths of the lower jawbones, with long, slender bones being low force but high velocity and short, thick bones providing strong biting forces but less speed during jaw closing.



The slingjaw wrasse, *Epibulus insidiator*, has the greatest jaw protrusion known among fishes. The jaw's bone and ligament structure, depicted here, comprise the lever action responsible for it. (Illustration by Jonathan Higgins)

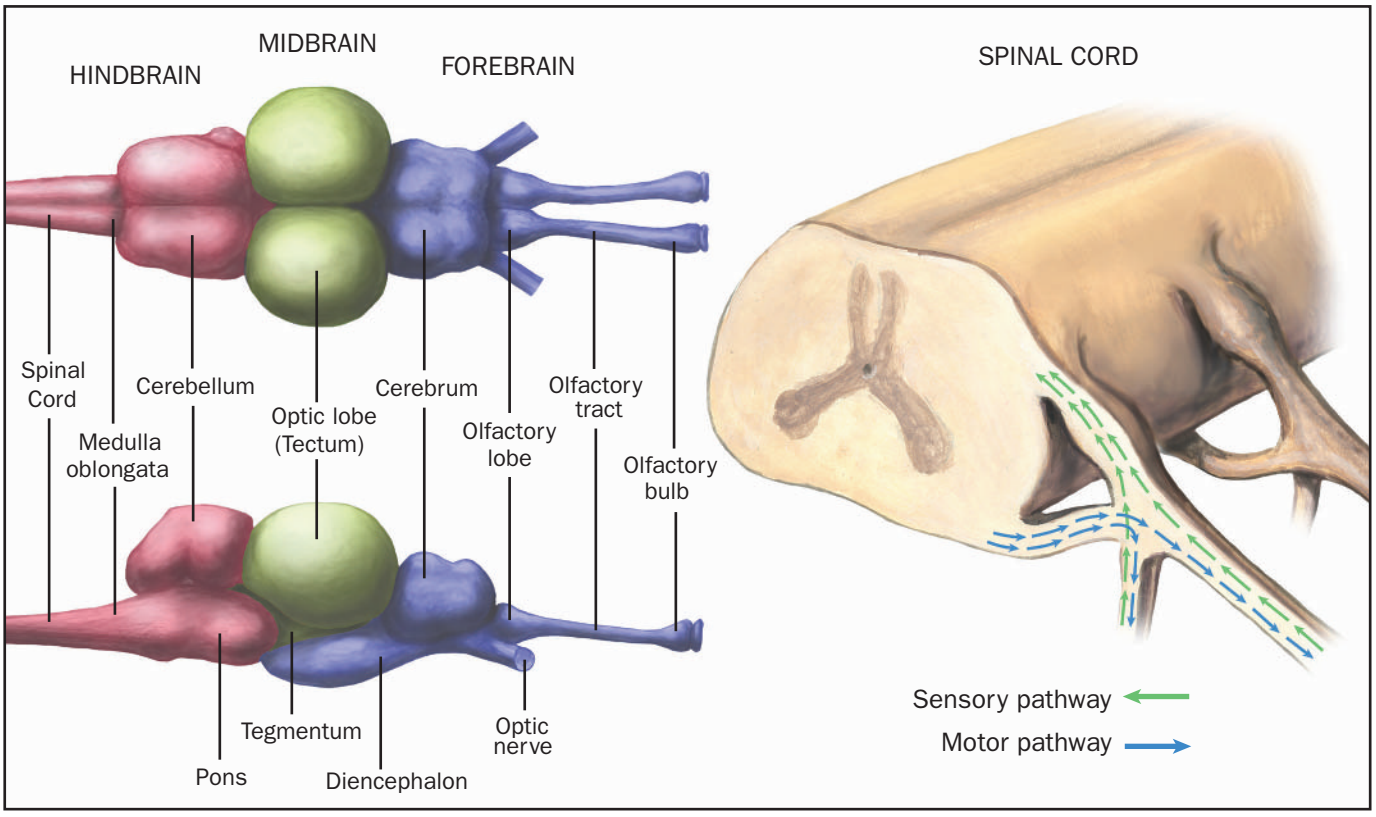
Close-up of a Port Jackson shark's (*Heterodontus portusjacksoni*) face. Port Jackson sharks feed primarily on invertebrates such as sea urchins, crabs, and starfish. (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

Teeth also vary markedly with a fish's prey. The teeth of predatory fish, including many carnivorous sharks, must cut through their prey and thus are triangular and serrated, providing effective blades for slicing through tissues. Other predators, including eels, which swallow prey whole, may have elongated backward-pointing teeth that are effective in grasping prey and preventing the prey from struggling out of the mouth. Many species have teeth adapted for biting or crushing hard material, such as shells or coral. Parrotfishes (family Scaridae) are named for their beaks, formed by fused teeth that function to bite hunks out of coral. Parrotfishes also have robust teeth on the pharyngeal jaws that contribute to the crushing of coral for digestion.

The action of the mouth and teeth (ingestion) is the first stage of digestion. From the buccal and pharyngeal spaces, food is moved through the esophagus to the stomach and intestine. The esophagus secretes mucus to help move food along its length, and it may stretch to accommodate large food items. The digestive enzyme pepsin and hydrochloric acid begin chemical digestion of the food and, in some groups, including mullets (family Mugilidae), the stomach may be modified into a grinding organ to continue physically processing food. The intestines vary in length among species, with the intestines of herbivores being substantially longer than those of carnivores. In addition, the surface area of the intestines may be increased for better internal absorption. Several organs are associated with the intestines. The pyloric caecae, liver, gallbladder, and pancreas produce enzymes and other substances that aid digestion in the intestines.

The axial system and locomotion

As suggested by their external morphological characteristics and functions, fins have diverse internal structures. Skeletal fin girdles support pectoral and pelvic fins, and the fins



Brain and spinal cord organization. (Illustration by Brian Cressman)

themselves consist of spines or rays that ar e connected by the fin membrane. Muscles at its base actuate the fin and, particularly with the pectoral fins, allow complex movement. Median fins also have skeletal support, with muscles that raise or lower the fins and segmentally arranged muscles on individual fin segments that allow for a wave of muscle activity to propagate along the fin. The caudal fin, which generates much of the thrust in axial swimming, is supported by a series of laterally flattened bones and associated muscles in addition to lateral body muscles. The caudal fin also is classified by the size of the dorsal and ventral caudal fin lobes. The most common designations are homocercal, in which the dorsal and ventral fin lobes are symmetrical (as in most bony fishes), and heterocercal, in which the dorsal and ventral lobes of the caudal fin are unequal in size. This type of tail is common in sharks but also is found in ray-finned fishes, such as the sturgeons and paddlefish (order Acipenseriformes).

Southeastern African lungfish (*Protopterus amphibius*) using its pelvic fin as a "leg." (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

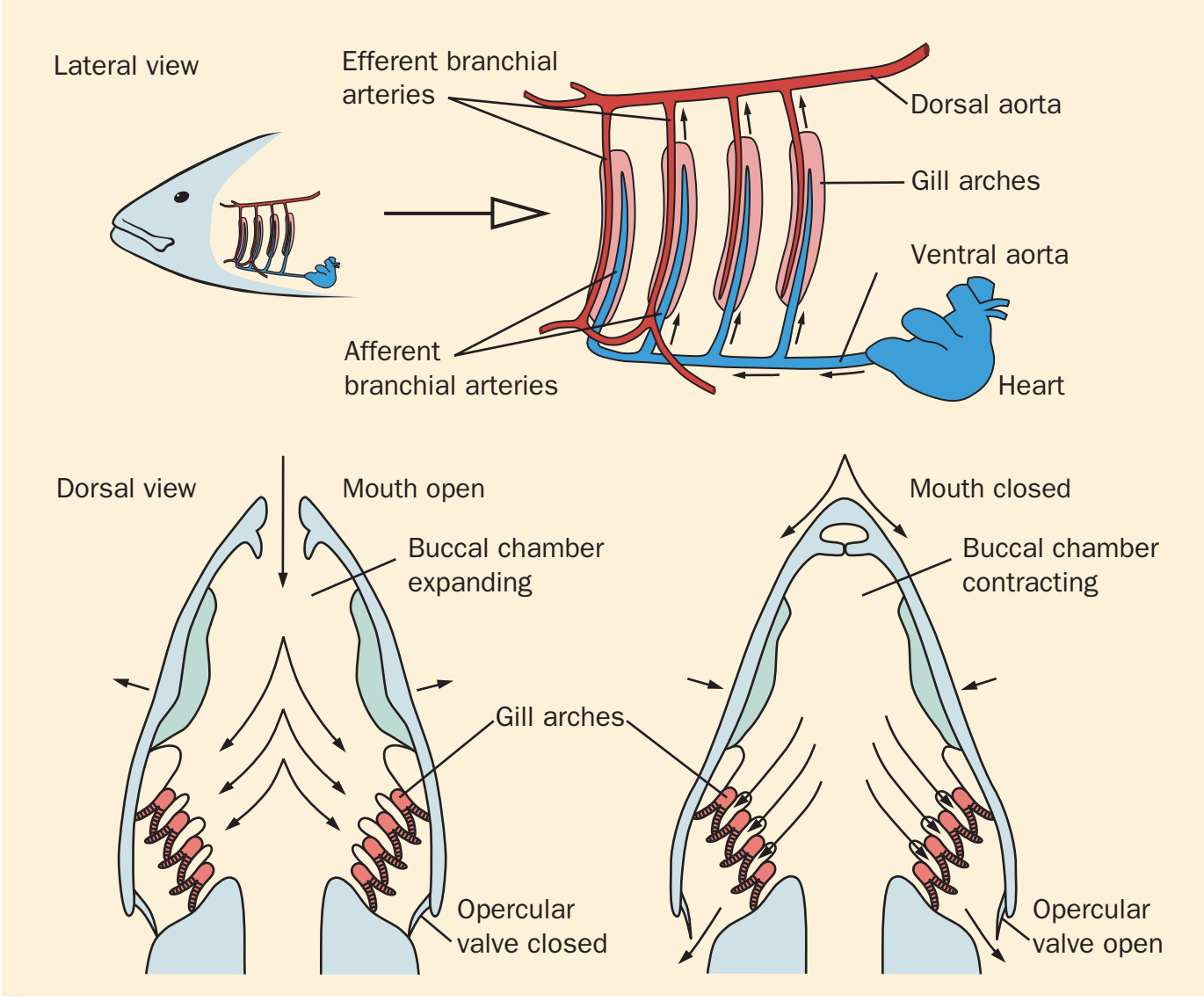
Vertebrae have several components. The centrum is the central structural element of the vertebra. The neural arch above the centrum protects the spinal cord. In the trunk region, lateral processes extend from the ventrolateral centrum. In the tail, processes form the haemal arch, which encloses the large dorsal aorta. The arches extend to form spines in the dorsal and ventral midlines, which, with connective tissues, shape the vertical septum that divides the left and right sides of the fish. Similarly, extending left and right from the vertebrae is the sheet of connective tissue called the horizontal septum, which divides the epaxial (dorsal) and hypaxial (ventral) regions of the lateral muscles, called the myomeres.

Axial swimming movements are accomplished by contractions of the myomeres that connect through tendons to the vertebral column. The myomeres are organized into interdigitating cones and bands of muscle separated by the connective tissue myosepta. Myomere contraction transmits force to the network of tendons, which bends the vertebral column. Rostral-to-caudal (head-to-tail) propagating waves of muscle

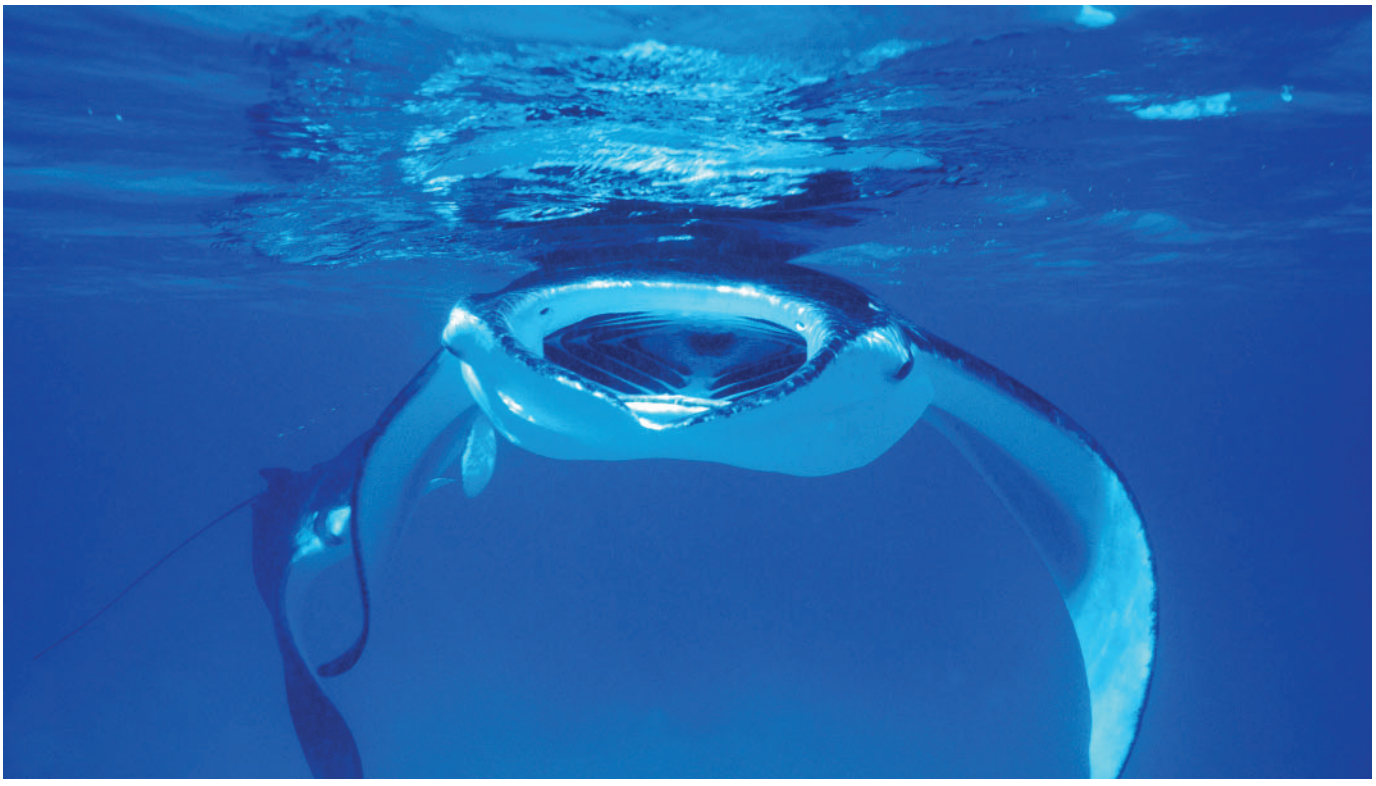
contraction generate the rostral-to-caudal waves of body bending during swimming.

The axial muscles often contain two common types of muscle fiber in fishes, each with a specific role in muscle function. Slow oxidative muscle functions in steady swimming. Slow muscles obtain energy through oxygen metabolism and are rich in myoglobin and vasculature that supplies oxygen, giving the muscle a red appearance. Because it is constantly supplied with oxygen, red muscle does not rapidly fatigue and thus can function in slow, sustained locomotion. Tunas and other large species that cruise steadily, searching for food, often have red muscle as a considerable proportion of their myomeres. In contrast to slow oxidative muscle, fast glycolytic muscle has a fast contraction time and uses glycogen stores as fuel. This type of muscle also is called white muscle, because with little vascularization and low levels of myoglobin, the muscle appears paler than oxidative fibers. Because glycogen stores are used up quickly, fast muscle fatigues quickly and functions primarily in short swimming bursts as, for example, when a fish is startled. In most fishes the white muscle forms the major mass of the myomeres.

In addition to generating movement of axis, fins, or cranial structures, muscles perform other functions in fishes. In some species muscles have adapted to act as thermoregulatory, or "heater organs." In tunas (family Scombridae) muscle activity keeps the brain warm while they feed for squid in cold, deep waters. Electrical currents generated during muscle contraction have been harnessed by elephantnose fishes as a communication signal or by torpedo rays as a tool for disabling other species. This modification of muscle cells into electrogenerative organs has evolved independently many times in the evolution of fishes, and there is considerable diversity in the muscles that serve this function, including eye muscles (stargazers, family Uranoscopidae), jaw



Flow of water and gas exchange through gills. (Illustration by Barbara Duperron)



The open mouth of a manta ray (*Manta birostris*) funnels food into its mouth while it swims, using two large, flap-like cephalic lobes that extend forward from the eyes. (Photo by Ivor Fulcher/Corbis. Reproduced by permission.)

muscles (torpedo rays), and axial muscles (electric eels, genus *Electrophorus*).

Neural control: The brain, spinal cord, and sense organs

The brain and spinal cord together form the central nervous system. The brain is subdivided into three regions—forebrain, midbrain, and hindbrain. The forebrain consists of the telencephalon and the diencephalon. At the rostral end of the telencephalon are the olfactory bulbs, which receive input from the olfactory receptors. The olfactory bulbs have neurons (the olfactory nerve, or cranial nerve I) that project into the olfactory regions of the telencephalon, also called the olfactory lobe because of its importance in this chemical sense. The olfactory bulb often is enlarged in fishes that rely heavily on olfaction, including many species of sharks. The diencephalon, which includes the epithalamus, thalmus, and hypothalamus, functions primarily in the regulation of the internal body environment. The pineal organ, which contains neurons and photoreceptors, is located at the distal end of the epiphyseal stalk and is part of the epithalamus, which projects from the dorsal surface of the diencephalon. In many species the pineal organ senses light through the cranium and may have numerous functions, including regulation of circadian rhythms. The optic nerve (cranial nerve II), which runs from the retina to the brain, enters the diencephalon and has inputs to the thalamus and hypothalamus as well as to the midbrain.

The midbrain consists of the optic lobe and tegmentum; both structures are involved in vision. The optic nerve has extensive connections to the optic lobe, and, as with the olfactory bulbs, a large optic lobe is associated with species that use vision extensively. The tegmentum functions in the control of intrinsic eye muscles to focus the visual image. The tegmentum also plays a part in motor control. For example, the midbrain locomotor region, which generates rhythmic swimming movements, is located in the tegementum.

The hindbrain includes the cerebellum, pons, and medulla oblongata. The cerebellum, unlike the more rostral brain regions, is a single structure rather than paired, bilateral lobes. The cerebellum's functions include maintaining equilibrium and balance. The pons and medulla form the brain stem. Many of the cranial nerves bring sensory information into the medulla and transfer motor signals to the muscles. Most of the cranial nerves enter the brain through the hindbrain. Cranial nerves III (oculomotor), IV (trochlear), and VI (abducens) control the six extraocular muscles that generate eye movements. Cranial nerve V (trigeminal) receives sensory input from and transfers motor signals to the mandible, and cranial nerve VII (facial) brings in sensory input from the hyoid arch and structures. Cranial nerve VIII (acoustic) contains sensory fibers that are involved in hearing and equilibrium. Cranial nerve IX (glossopharyngeal) serves the pharyngeal arch, providing both sensory information and motor output. Cranial nerve X (vagus) innervates the more caudal branchial arches as well as the lateral line and viscera.

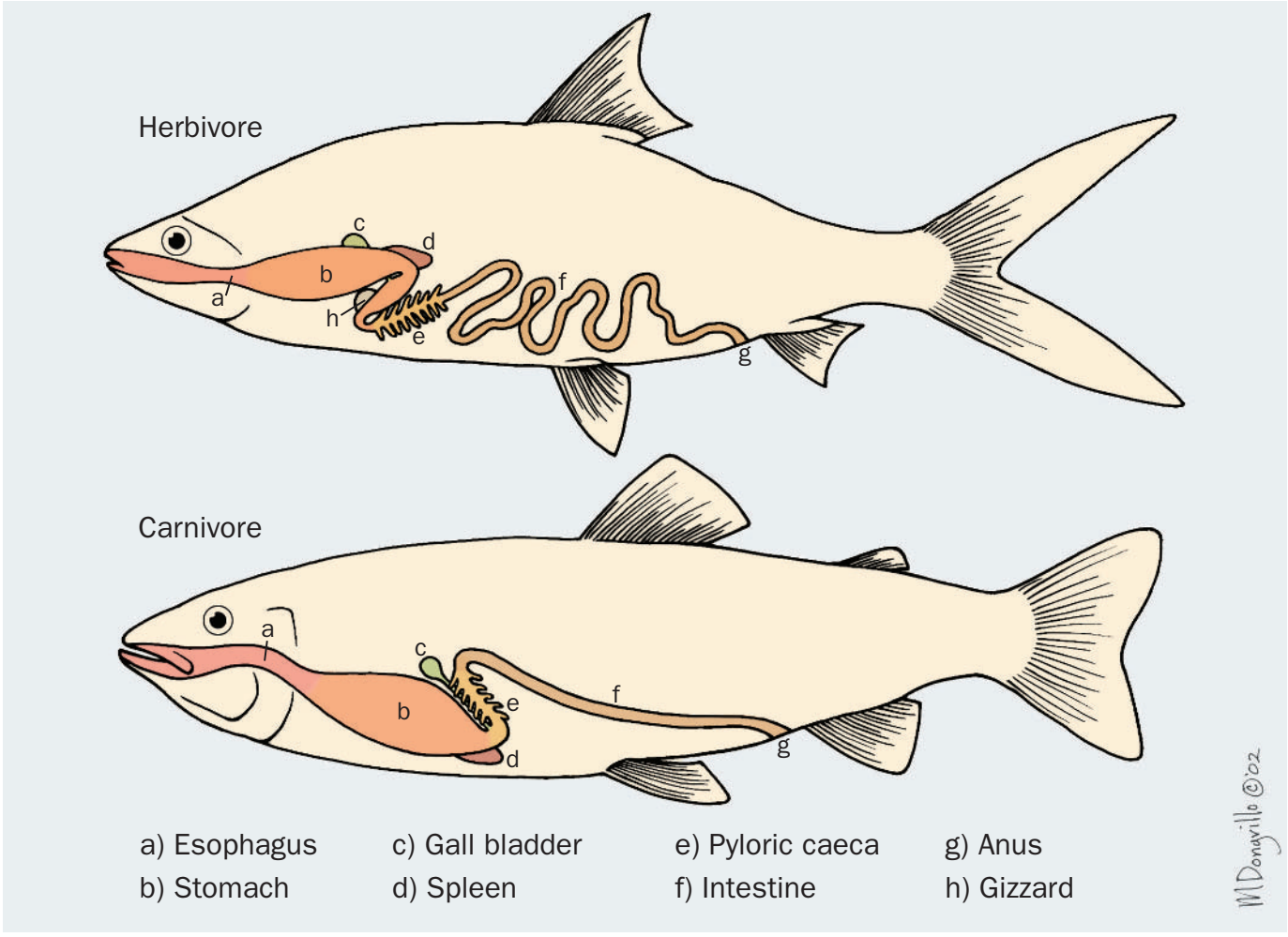
The spinal cord runs the length of the vertebral column, protected by the neural arch. As with the myomeres and ver-

tebrae, the spinal cord is organized segmentally. At each body segment, sensory neurons enter the cord through the dorsal roots, and motor neurons exit through the ventral roots. Interneurons, located entirely within the central nervous system, carry information between sensory and motor neurons and relay information to and from other interneurons in the brain.

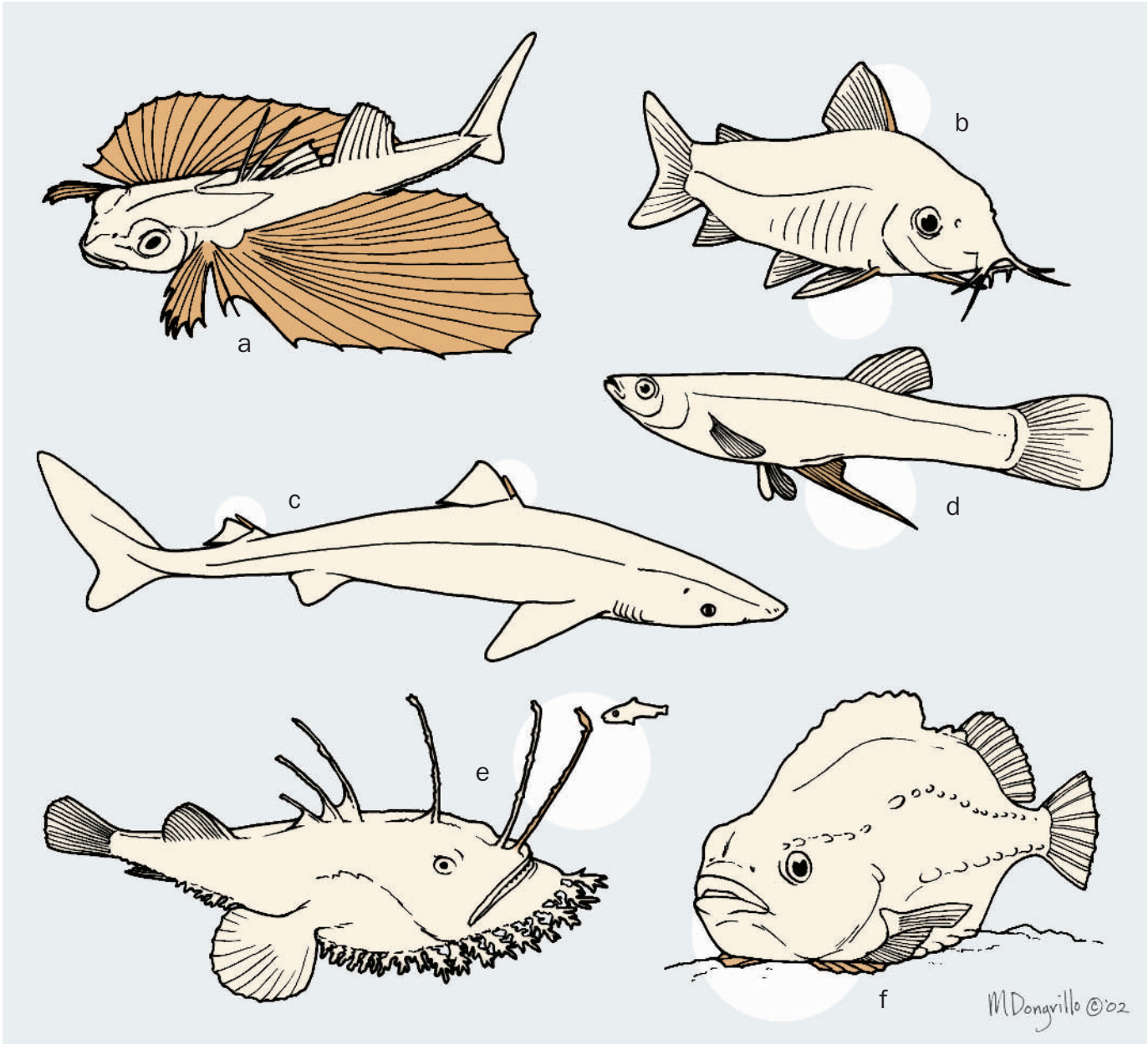
The nervous system takes in sensory information and processes it to derive an appropriate response. Fishes use a wide array of senses to survey their environments. Vision is one of the best-understood sensory systems. The eyes of fishes are very similar in structure to the eyes of other vertebrates, with light coming in through the cornea and lens and projecting onto the retina, where rods, cones, and other nerve cells receive, process, and transmit the visual image. Instead of changing the shape of the lens, fishes focus the often near-spherical lens by moving it closer to or farther away from the retina. The organization and composition of the retina vary with a fish's visual environment. Deep-sea fishes have visual pigments that absorb light maximally in lower, blue wavelengths, while shallow-water species absorb a broader distribution of the light spectrum.

Eye position is also indicative of a fish's way of life. Bottom-dwelling predators that surprise prey from below, such as flatfishes or stonefishes, have eyes positioned upward and close together to provide binocular vision. Prey species generally have eyes positioned laterally to best survey for predators. *Anableps*, the four-eyed fish, lives at the surface of the water. It has four pupils to take in light dorsally through air and ventrally through water. The lens is shaped and positioned to focus the light from two sources on two regions of the retina, allowing for simultaneous input from both visual environments.

Both smell and taste permit fish to sense chemical signals. That fish may have an extremely well developed ability to sense chemical signals is illustrated in salmon and trout, which distinguish their natal streams based on chemical cues. Whereas olfactory receptors are localized in the olfactory epithelium within the bilateral nares, taste receptors, or taste buds, are more widespread, occurring not only in the mouth but also frequently on the gill structures and external surfaces, including the barbels, fins, and skin. Signals from the taste buds are transmitted to the brain through several cranial nerves. Cutaneous receptors have input through the facial nerve, whereas inputs



Differences in digestive systems between herbivorous and carnivorous fishes. Although most structures are the same, the herbivore has a gizzard, as well as a longer intestine. (Illustration by Marguette Dongvillo)



Fin morphology of fishes: a. Sea robin (*Dactylopterus volitans*): b. Catfish (*Corydoras aeneus*); c. Piked dogfish (*Squalus acanthias*); d. Mosquitofish (*Gambusia affinis*); e. Anglerfish (*Lophius piscatorius*); f. Lumpfish (*Cyclopterus lumpus*). (Illustration by Marguette Dongvillo)

from receptors in the mouth travel to the brain through the glossopharyngeal and vagus nerves. These nerves lead to the brain's medulla, and, as with olfaction, fishes that use taste extensively to find prey have enlarged regions of the medulla corresponding to cranial nerves VII, IX, or X.

The primary mechanoreceptive systems are the ear, functioning in hearing and equilibrium, and the lateral line that senses contact at the surface of the body. The inner ears of elasmobranches and bony fishes are organized into three semicircular canals and three chambers, each containing an otolith, or ear stone, that rests on sensory hair cells associated with nerve cells. Two of the chambers, the saccule and the laguna, function in hearing. Vibrations from the environment lead to movement of the chambers and the otoliths. The difference in movement is sensed by the hair cells and is processed as hearing. Ostariophysan fishes, including goldfish, catfishes, and others, have a series of bones called Webberian ossicles that connect the ear to the swim bladder. Vibrations are amplified through the swim bladder and improve hearing at high frequencies. Similarly, an otolith in the third chamber, the utricle, allows the fish to sense orientation in the water. This dense otolith lies upon sensory hair cells. When the body tips and the otolith moves, stimulation to those cells changes as well, signaling the change in orientation.

The sensory hair cells in the semicircular canals allow fishes to sense orientation and acceleration. Each canal is as-

sociated with an ampulla in which hair cells are located. Instead of an otolith, gel covers the cells. When fluid, called endolymph, in the semicircular canals moves as the result of a change in acceleration of the fish, the endolymph moves the gel and thus stimulates the sensory cells. The three semicircular canals are positioned approximately at right angles to one another to sense vertical, lateral, or forward movement.

Water movement on the surface of the fish is sensed through neuromasts. These structures can be found individually on the surface of the body, or they may sit below scales in canals called lateral lines. Neuromasts include a cupula of gel consistency and sensory hair cells, which project hairs into the cupula and synapse with nerve cells below the surface of the body. Movement of the cupula causes the hair cells to deflect, signaling a perturbation of the fluid around the fish.

Electroreception occurs in many groups of fishes and has numerous functions, including sensing murky environments; sensing prey, such as fishes that sleep buried in sand; or, in species that also generate electrical signals, receiving signals from other animals. Electrical input is received in pit organs on the surface of the body. Pit organs are filled with gel that conducts electrical current and, at their base, contain electroreceptor cells that synapse with sensory neurons.

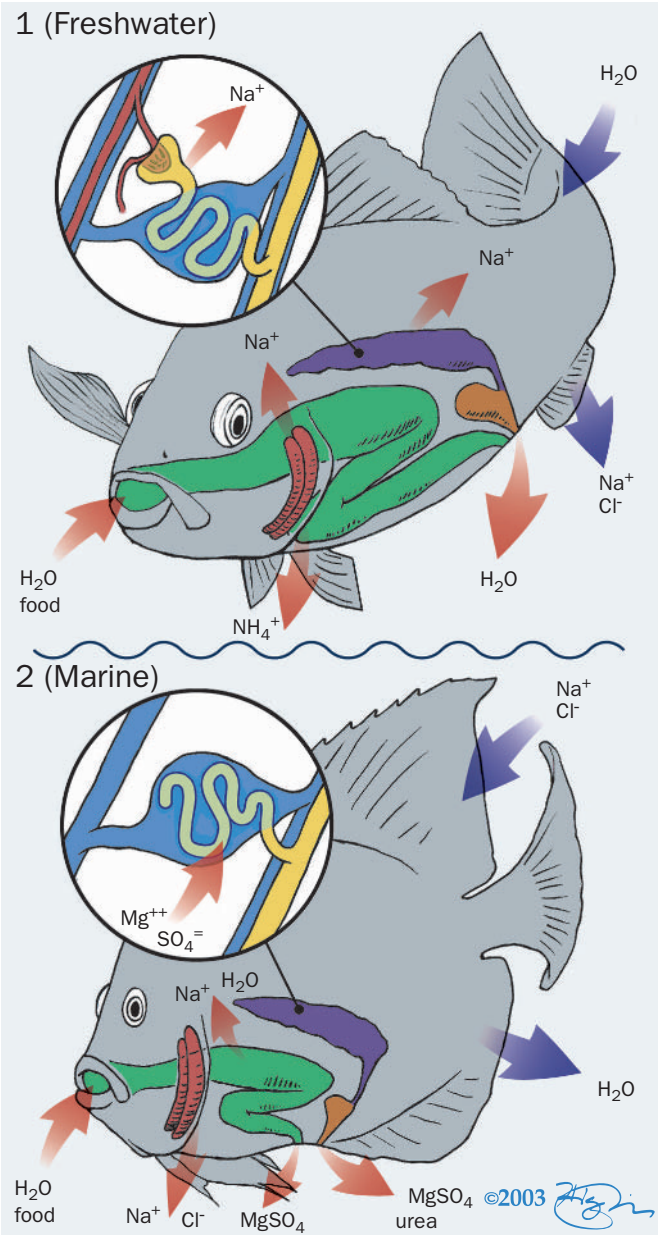
Homeostasis

The autonomic nervous system and the endocrine system function together to regulate an animal's physiology. The autonomic nervous system, which includes a series of ganglia lateral to the spinal cord, receives input from the central nervous system to adjust the function of numerous tissues. Blood pressure is regulated through vasodilation or vasoconstriction, affecting numerous functions from digestion to oxygen uptake at the gills. The endocrine system similarly has broad effects on physiology, but through hormones rather than nerve activity. Controlled primarily through the hypothalamus and the pituitary, the endocrine system has many functions, including osmoregulation, growth, and metabolism.

Circulation and gas exchange

The circulatory system carries blood from the heart through the gills and to the body tissues before returning to the heart. The fish heart is unlike the mammalian heart, where left and right sides function to take deoxygenated blood from the body to the lungs and separately take deoxygenated blood from the lungs to the body. The heart of fishes is a single series of four chambers, with deoxygenated blood running through the heart to the gills and straight out to the body without returning to the heart. The four chambers of the heart are the sinus venosus, atrium, ventricle, and conus arteriosus. The chambers of the heart are separated by valves to prevent blood from flowing in the wrong direction during ventricular pumping.

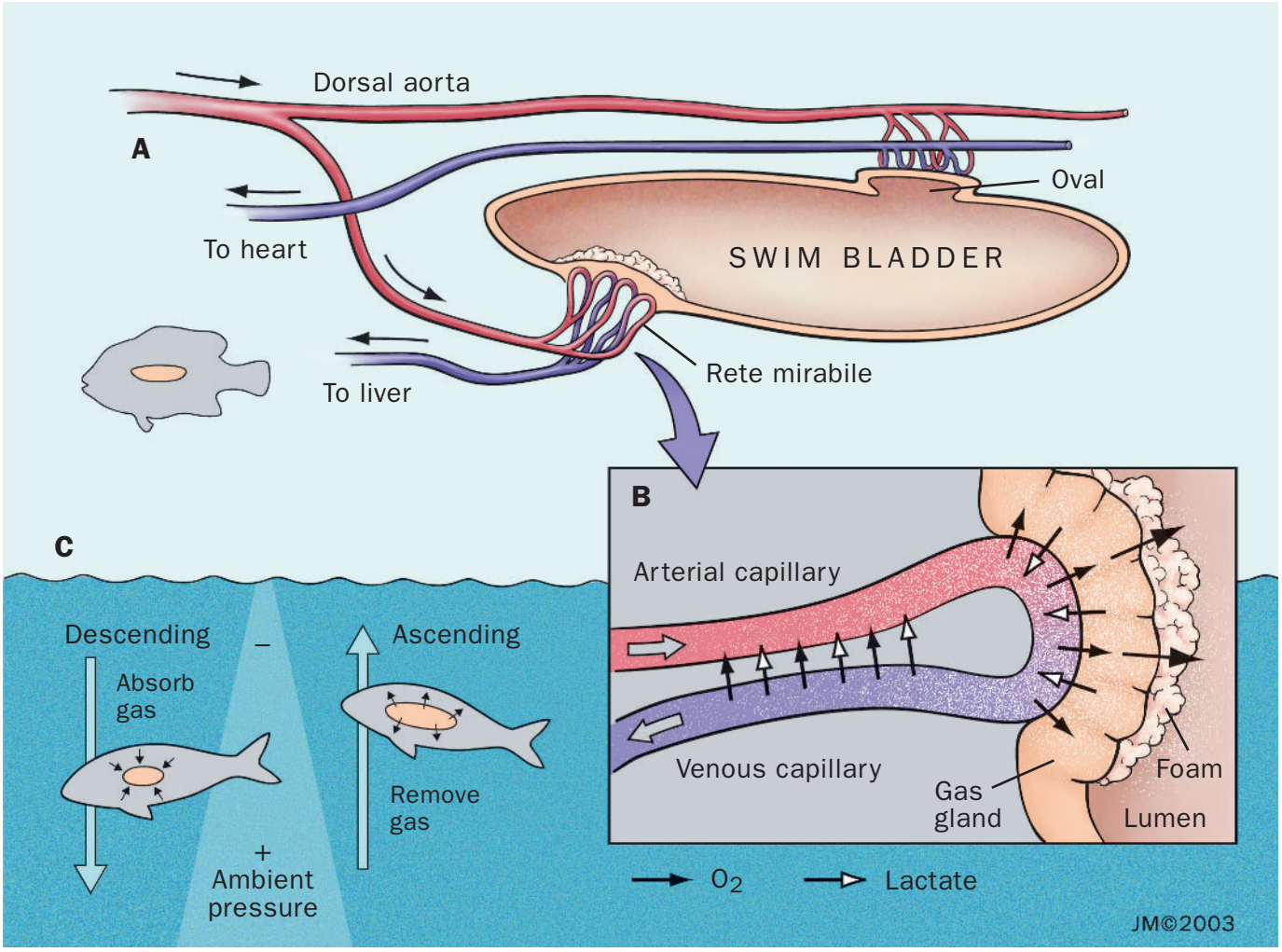
The gills are the primary respiratory organs of fishes. Gills are located lateral to the mouth cavity. In bony fishes, they are covered by the opercula. Chondricthyan fishes and lampreys do not have an operculum; instead, each gill vents to the surface of the body individually through gill slits. During ventilation, water flows into the mouth, across the gill, and through the gill slits or opercular opening. When negative



Osmoregulation/homeostasis in freshwater and marine fish. (Illustration by Jonathan Higgins)

pressure is generated in the mouth, the opercula or gill slits close over the gills to prevent water from flowing into the mouth through the opercular openings. The gills are formed from membranes and blood vessels lying over branchial arches. On each arch, lamellae project outside the buccal cavity. The lamellae have smaller processes called secondary lamellae, which are highly vascularized for oxygen exchange.

Fishes have a diverse array of other respiratory structures in addition to the gills. In larval fishes, gas exchange commonly occurs across the skin. Many fishes have accessory breathing organs. Numerous fishes have "lungs" in which air is stored. These fishes include many basal bony fishes, such as bowfins (order Amiiformes), gars (order Lepisosteiformes),



Structure and function of the swim bladder. The fish becomes less buoyant (descends) as gas is absorbed into the bloodstream and leaves the swim bladder. The fish ascends as gas is removed from the bloodstream and enters the swim bladder, enlarging it. (Illustration by Jacqueline Mahannah)

and reedfish (order Polypteriformes), which gulp air at the surface of the water. Several species that can breathe air include some catfishes (genus *Clarius*) and gouramis (family Osphronemidae), which have evolved structures associated with the gills for this function

Buoyancy control in the fluid environment

Gas exchange also occurs in the swim bladder, a sac full of gases that lies dorsally in the body cavity and functions primarily in buoyancy control. An increase in the amount of gases in this structure makes fish more buoyant, and a decrease makes them less buoyant. In many fishes, gas can enter the gas bladder only through the gas gland and rete mirabile ("wonderful net"), a highly vascularized tissue that, as in the gill filaments, provides a large surface area for gas exchange. The gas gland acts by acidifying the blood, decreasing the solubility of dissolved gases and thus increasing the available molecules for exchange into the swim bladder. A membrane called the oval controls the amount of gas in the bladder. Unlike the rest of the bladder, which is lined with the amino acid guanine to prevent resorption of gases, the oval is highly permeable. The loss of gas from the bladder through the oval is controlled by muscles that can either obstruct the oval, preventing gas release, or free it for gas exchange. Some fishes have a pneumatic duct that runs from the alimentary canal to the swim bladder. This allows them to gulp air at the surface and store it in the gas bladder.

Many fishes have other adaptations to make them more buoyant, including morphological structures that are built for lightness. Some groups, including chondrichthyan fishes, do not have swim bladders and instead augment their buoyancy with fat stores. Another strategy in negatively buoyant fishes may be to alter body movements during locomotion to produce lift and upward thrust as well as forward thrust.

Osmoregulation and excretion

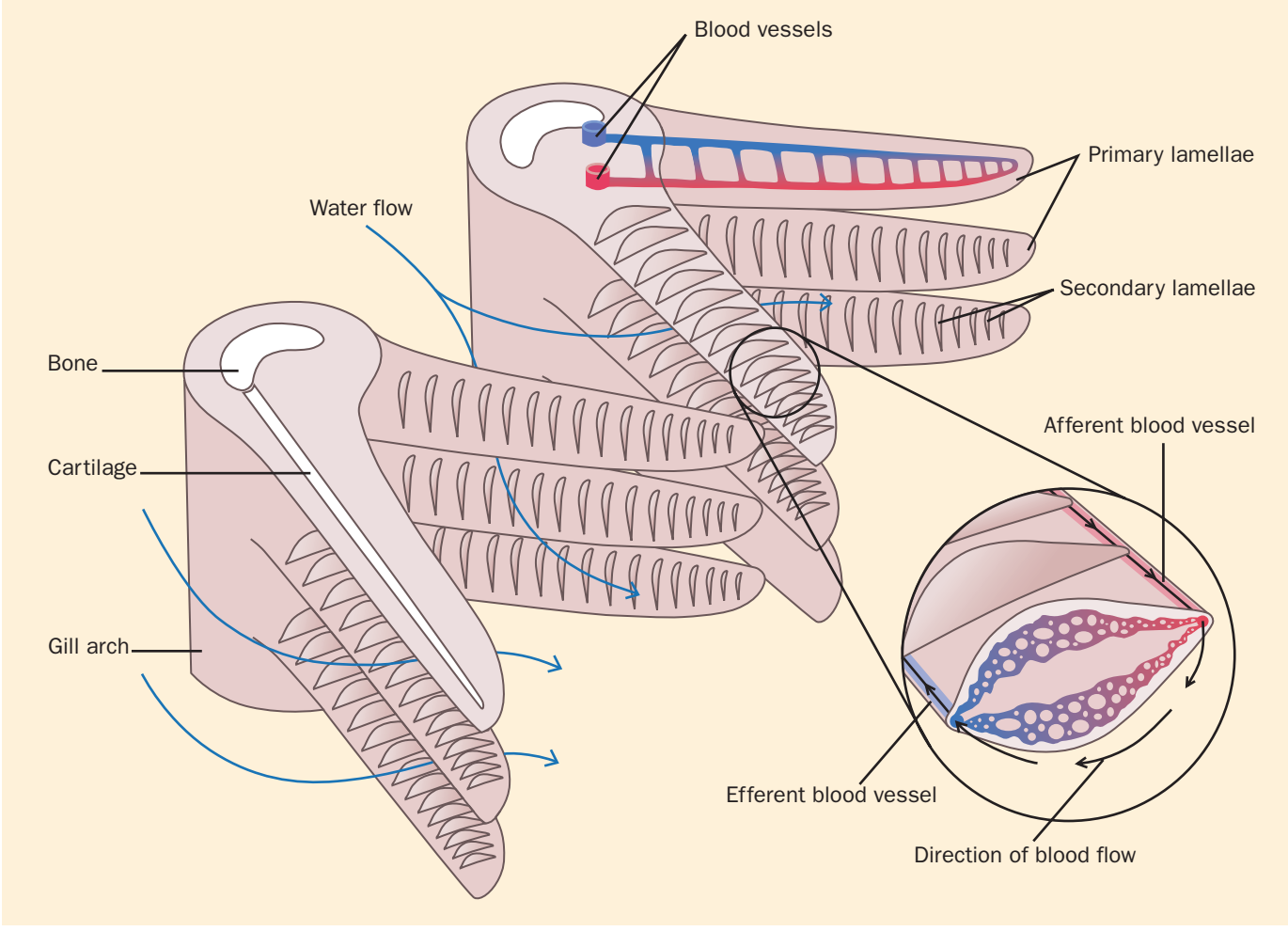
Living in water provides a set of challenges for osmoregulation, and fishes have developed a diverse array of strategies for manipulating their osmotic concentrations of various

substances. Almost all fishes maintain osmotic levels that are lower (saltwater fishes) or higher (freshwater fishes) than the fluid in the environments around them. The lone exception is the hagfishes (family Myxinidae). Hagfishes, one of the most basal lineages of vertebrates, have internal salt concentrations at about the level of seawater, as do marine invertebrates. Marine elasmobranchs (sharks, rays, and skates) are isosmotic but with substantially lower salt concentrations in their bodies. They maintain this balance by retaining high concentrations of urea and trimethyl amine oxide (TMAO) in the blood. The urea increases the osmotic concentrations to the level of seawater. To keep salt concentrations low relative to the environment, elasmobranchs secrete salt through the kidneys and a special gland, the rectal gland, which connects to the alimentary canal. The rectal gland concentrates and eliminates both salt and chloride ions from the body tissues.

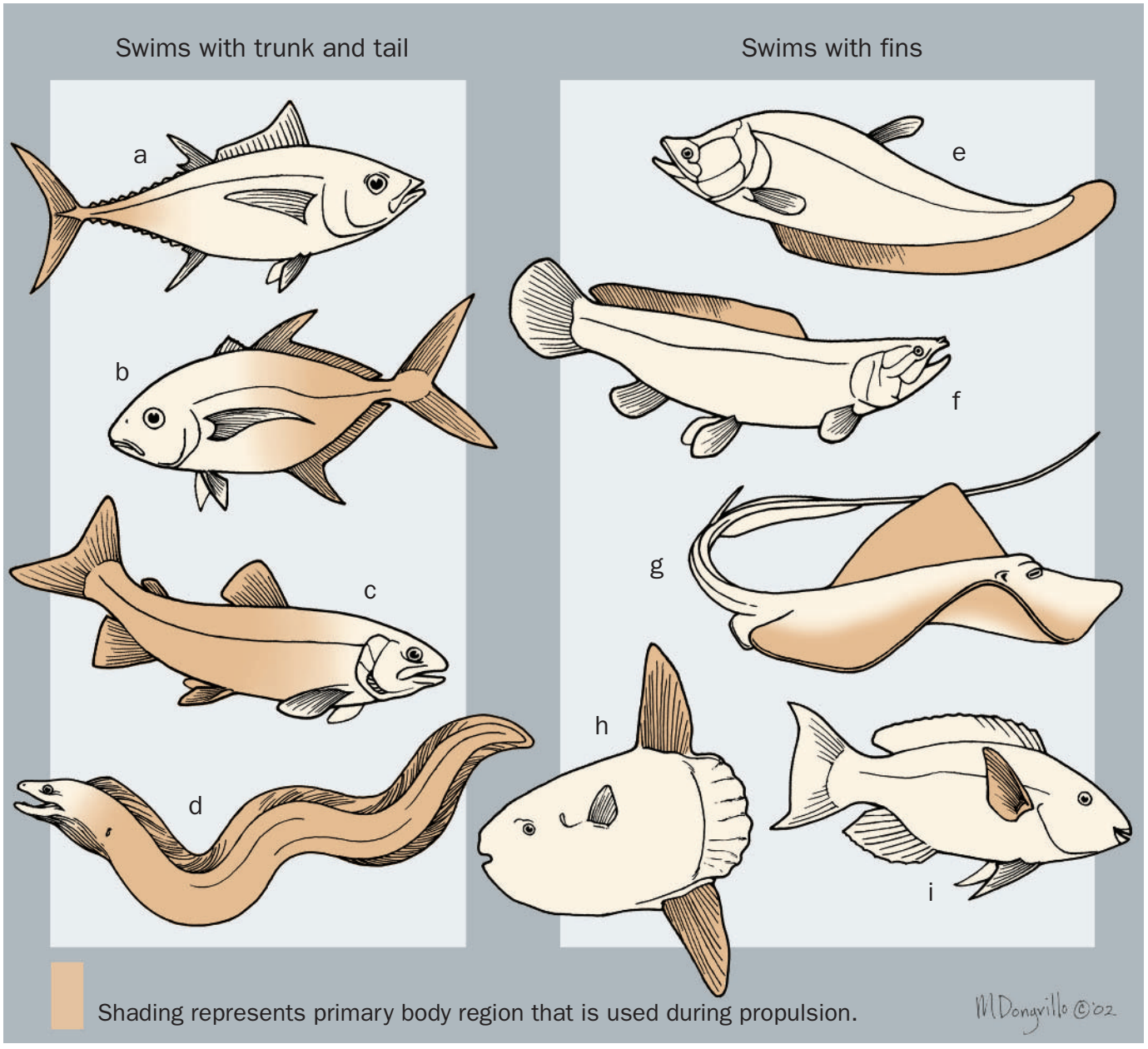
Teleost fishes are not isosmotic and have evolved mechanisms to regulate retention or elimination of ions. Marine teleosts with lower ionic concentrations than the fluid that surrounds them are constantly loosing water to the environment. They counter this loss by drinking and filtering saltwater. Salt and chloride ions are transported from the blood through the gill membranes, while magnesium and sulfates are filtered from the blood by the kidneys. Freshwater teleosts have the opposite problem of maintaining salts in an environment where the normal concentrations are low. In particular, water can move into the bloodstream through the alimentary canal and the gills, diluting internal concentrations. Again, the gills and the kidneys are critical to this balance. The gills actively take up some solutes from the water, and freshwater teleosts produce copious amounts of dilute urine.

Reproduction

Fishes demonstrate a wide range of reproductive strategies. Fishes may be males, females, or, in many species, hermaphrodites, with both male and female sex organs. There are several types of hermaphroditism, and simultaneous hermaphrodites may act as both male and female in a single breeding event. Hamlets, small species of sea bass (family Serranidae), breed in pairs, with individuals taking turns as male and female. Other simultaneous hermaphrodites, including numerous deep-sea species, are self-fertilizing. Serial hermaphrodites may be female at one time in their life history



Microstructure of gills, showing water flow and blood flow. (Illustration by Barbara Duperron)



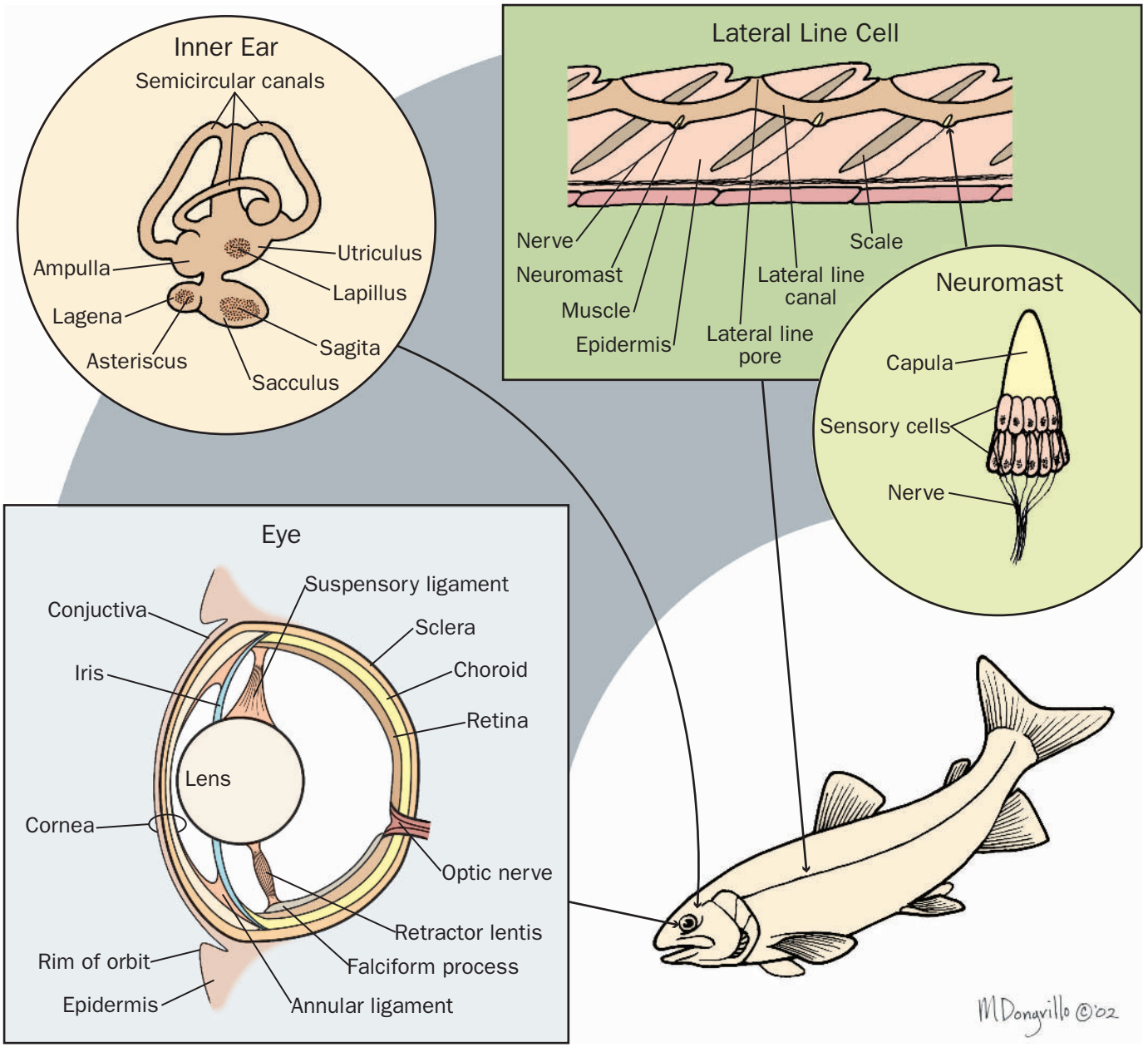
Fishes' body and fin shapes determine their type of locomotion: a. Thunniform locomotion, bigeye tuna (*Thunnus obesus*); b. Carangiform, blue trevally (*Carangoides ferdau*); c. Subcarangiform, rainbow trout (*Oncorhynchus mykiss*); d. Anguilliform, green moray (*Gymnothorax funebris*); e. Gymnotiform, clown featherback (*Chitala ornata*); f. Amiiform, bowfin (*Amia calva*); g. Rajiform, southern stingray (*Dasyatis americana*); h. Tetraodontiform, mola (*Mola mola*); i. Labriform, bridled parrotfish (*Scarus frenatus*). (Illustration by Marguette Dongvillo)

and male at another. Protandrous species, including some damselfishes (family Pomacentridae), are first male and then become female as they age. Protogynous species, including many wrasses (family Labridae) and other perciformes, on the other hand, begin as females and become males. One of the more unusual strategies is that demonstrated by several families of anglerfishes. Smaller, parasitic males latch onto females with their mouths and fuse permanently with the female's body. The male obtains nutrition through the female' bloodstream and provides sperm for reproduction. Males of the seahorses and pipefishes (family Syngnathidae) have pouches or specialized body surfaces that hold eggs while the embryos are developing.

Despite these variations in modes of reproduction, the basic reproductive structures are similar among taxa, with eggs being produced in the ovaries and sperm being produced in the testes. Ovaries and testes are held in places in the abdomen with mesenteries—the mesovaria for ovaries and mesorchia for the testes. The paths that the sperm and eggs take vary among species. Sperm or eggs may be released into

the body cavity, as in Agnathans (lamprey and hagfish), and leave through pores in the abdomen. However, in most species, eggs are carried in the oviducts, which may be continuous with the ovary—as in many teleosts—or may be separated by a small space across which the eggs travel.

While in most fish species eggs and sperm are released by the parents and fertilization and development occur externally, a number of groups of bony fishes as well as sharks and other species in the class Chondrichthyes have internal fertilization. Sharks demonstrate a range of parental care prior to laying eggs or birthing pups. Many species, including skates (order Rajiformes), are oviparous, with the embryo relying completely on its yolk for sustenance. Oviparous species lay eggs that develop externally to the mother. In ovoviviparous species, such as the whale shark, the embryos depend on the yolk for nutrition but remain inside the mother through the embryonic period. Embryos hatch within the mother and are born free-swimming. Viviparous species similarly retain their embryos, but those embryos obtain nutrition both from the yolk sac and from the mother. Nutrition from the mother may be obtained via a placental structure connected to the mother's circulatory system, as in hammerheads (family Sphyrnidae), or from nutrient-rich fluids secreted by cells of the uterus, as in manta rays (*Manta birostris*).



Sense organs of fishes visual, auditory, and lateral line systems. (Illustration by Marguette Dongvillo)

Resources

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Melina Hale, PhD

Life history and reproduction

Types of reproduction

The vast array of adaptations that has evolved in fishes has given them the ability to inhabit a wide range of different habitats, including open seas and oceans, lakes, ponds, estuaries, rivers, tide pools, springs, deserts, forests, mudflats, and mountains. In addition, they have evolved the ability to exist in extreme areas with regard to temperature (e.g., the Antarctic), low oxygen, pH, and tremendous pressure. In fact, fishes exhibit the greatest vertical distribution of any group of vertebrates. As the result of selective pressures associated with these different environments, fishes have evolved three types of reproduction: bisexual, hermaphroditic, and parthenogenetic.

Bisexual

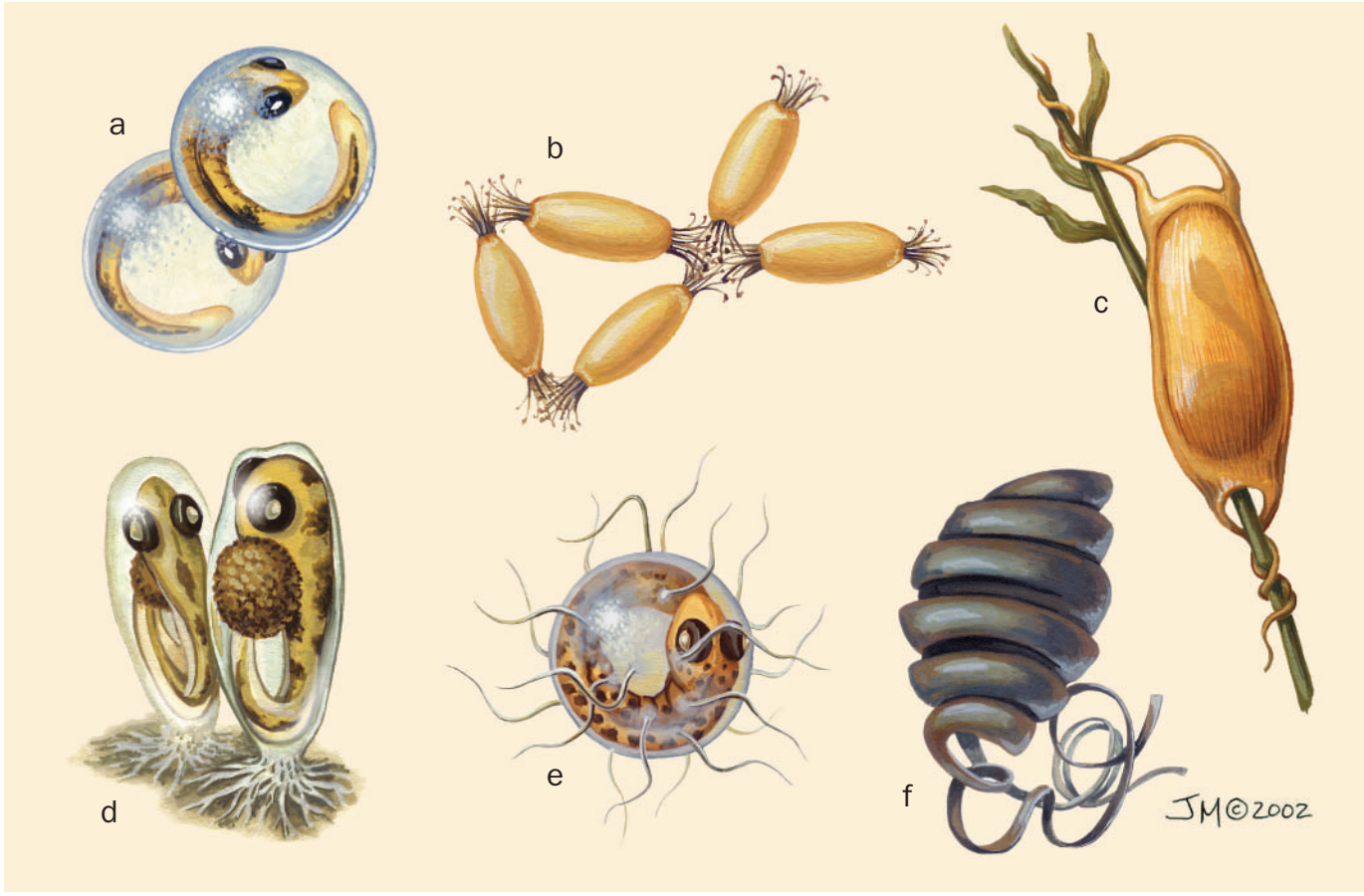
Bisexual reproduction is the most common form observed in fishes. In this type of reproduction, the sexes are separate ("dioecious") within the species. Species that are involved in bisexual reproduction may exhibit slight to very pronounced secondary sexual characteristics, or sexual dimorphism. Characteristic of these secondary sexual traits is that they usually are expressed in only one sex (typically the male), do not occur until maturation, may intensify during the breeding season, and generally do not enhance individual survival. Secondary sexual traits may consist of differences in body size, body parts (e.g., elongated fins), body ornamentation (e.g., nodules on the head), dentition, color pattern, and body shape and, possibly, differences in acoustic, chemical, and electrical attributes between the sexes. Bisexual mating systems include monogamy, polygamy, and promiscuity.

Hermaphroditic

The second type of reproduction in fishes involves sex reversal, where fishes function as male or female simultaneously or sequentially. Sequential hermaphrodites function as males during one part of their lives and females during another. There are two distinct forms of sequential hermaphrodites—protandric and protogynous. Protandric hermaphrodites are individuals that start out as male and later in life undergo internal morphological changes and become fully functional females. Protandric hermaphrodites are widespread among the sea basses (Serranidae). All wrasses (Labridae) appear to be protogynous hermaphrodites, in that all males are derived from females. Environmental factors or, more specifically, social cues influence sex change in wrasses. The social system adopted by wrasses consists of a harem of females and one large male. The entire group is structured according to size, with the male at the top of this hierarchy. If a female is removed from the harem, the other females maneuver within the hierarchy. All the smaller females typically move up one position. If the male is removed or dies, the largest female in the harem attempts to fill the male's position by aggressively warding off neighboring males. If she is successful, within several hours she will display the male's behavior and will court and spawn (with no sperm released) with the subordinate females after two to four days. After approximately 14 days she becomes a fully functional male. In those taxa where sex reversal is mediated by social cues, the process varies widely, and a single individual can change from one sex to the other several times in response to these cues. On the other hand, there are many taxa (e.g., stripped bass, yellow perch, most groupers) of sequential hermaphrodites in which sex change occurs independently of social cues.

Simultaneous hermaphrodites possess a functional ovotestis and are capable of releasing viable sperm and eggs; hence, they have the potential to fertilize their own eggs. Only three species of cyprinodontiform fishes (*Cynolebias* species and *Rivulus marmoratus*) are known to be self-fertilizing hermaphrodites. Self-fertilization of *R. marmoratus* is internal and results in homozygous, genetically identical individuals. Because

California bullhead shark (*Heterodontus francisci*) eggcase. About 25% of all shark species lay eggs. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)



Diversity of external egg characteristics: a. Cod eggs; b. Hagfish eggs; c. Catshark eggcase; d. Gobie eggs; e. Flyingfish egg; f. Bull shark eggcase. (Illustration by Jacqueline Mahannah)

many cyprinodontiform fishes inhabit harsh habitats, self-fertilization may be a reproductive strategy to ensure mates in low-density and isolated populations. The more common pattern of simultaneous hermaphroditism is seen among the hamlets (*Hypoplectrus* and *Serranus*). Although these fishes are capable of producing both sperm and eggs at the same time, they function as only one sex at a time during a spawning event. Because some spawning events may last several hours (e.g., in hamlets), members of a pair may alternate sex roles, with one individual playing the part of the male and releasing sperm and later taking the role of the female and releasing eggs.

Parthenogenetic

Although it is rare in vertebrates, parthenogenetic reproduction does exist in a few species of fishes. By definition, parthenogenetic reproduction involves complete development of an egg without fertilization by a sperm of the same species. A variation on this type of reproduction exists in fishes. In fishes, mating with a heterospecific or conspecific male is required. The role of the male is in providing an active sperm, which comes in contact with the egg but which does not penetrate the egg membrane (chorion). The sperm acts as a stimulus for the egg to begin developing. The sperm does not contribute to the genetic makeup of the resulting fry. The fry is genetically identical to the female; hence, males are never produced by parthenogenetic reproduction. The best-studied example of this phenomenon are live-bearing top minnows of the genus *Poeciliopsis*.

Modes of reproduction

In addition to the three different types of reproduction, there are three developmental modes of reproduction: oviparous, ovoviviparous, and viviparous.

Oviparous

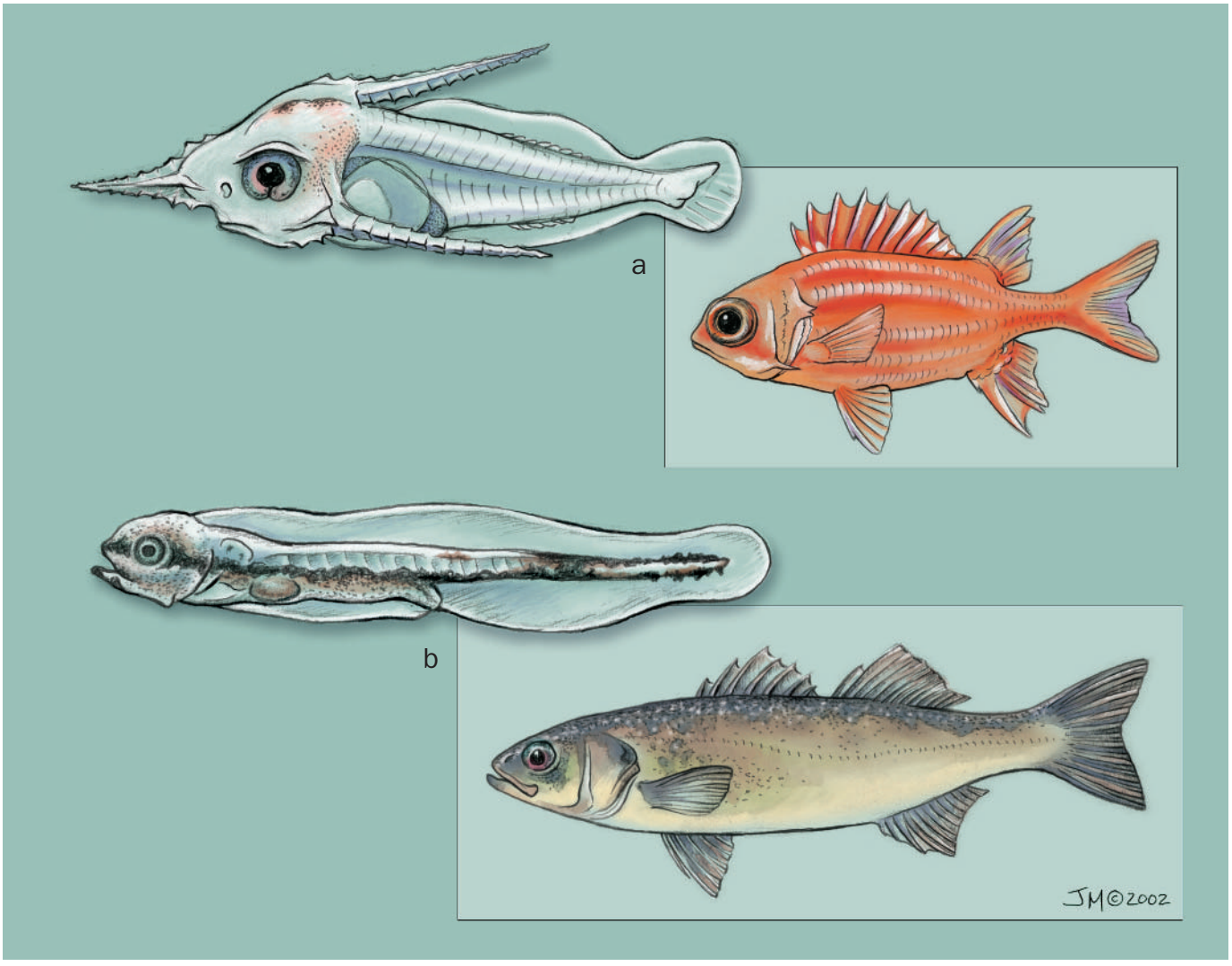
Oviparous reproduction typically involves the release of both male and female gametes into the surrounding water, where fertilization takes place. Fertilization is internal in numerous fishes (e.g., rockfishes of the family Scorpaenidae and Neotropical catfishes of the family Auchenipteridae), however, and is followed by the often delayed release of embryonated eggs by the female into the surrounding environment. Upon fertilization, the developing embryo uses both yolk reserves and oil droplets as nutrients. In the marine environment, the eggs are generally buoyant and float in the upper water column for varying periods of time before undergoing metamorphosis and settling out of the plankton community. The resulting larva, in many cases, differs drastically from the adult and may spend considerable time floating in the water. Species that exhibit this mode of reproduction usually produce large quantities of small eggs owing to a high mortality rate.

While the vast majority of marine fishes are oviparous (including both pelagic and reef species), commonly with a planktonic stage, most freshwater fishes that have oviparous reproduction lack this stage, producing fry that closely resemble the adults. In addition, not all oviparous fishes produce buoyant eggs; instead, some produce demersal eggs (most freshwater fishes) that may have adhesive properties. The adhesive quality allows them to stick to rocks and plants, thus preventing them from washing away. Demersal eggs very often are associated with parental care, which is extremely widespread among fishes. Although oviparous species produce the greatest number of eggs, these eggs and the resulting larvae are very small.

A clown triggerfish (*Balistoides conspicillum*) guarding eggs (the yellow-green mass) near Menjangan Island, part of Bali Barat National Park in Bali, Indonesia. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Ovoviviparous

In ovoviviparous reproduction the eggs are retained by the female, and fertilization is internal. Although the eggs are retained, there is no placental or blood connection between the developing embryos and the female. Instead, the



Larval diversity in fishes. a. Squirrelfish (*Sargocentron vexillarium*) larva, left, is 0.19 in (4.7 mm) in length. Adult is shown on the right. b. European sea bass (*Dicentrarchus labrax*) larva, left, is 0.24 in (6 mm) in length. Adult is shown to its bottom right. (Illustration by Jacqueline Mahannah)

Gravel flies as a female brook trout uses her tail fin to dig a redd (nest) in the Pleasant River in Windham, Maine. A male stands guard over the nest at rear. When the hole is sufficiently deep, the pair will come alongside each other. The female will then deposit her eggs while the male fertilizes them with his milt. (Photograph. AP/ Wide World Photos. Reproduced by permission.)

embryos develop completely within the egg, where all the necessary nutrients are present before hatching. Upon reaching full term, the embryos hatch inside the female, after which they are immediately born alive in the surrounding water. Those species that exhibit ovoviviparous reproduction do not have a pelagic stage, instead producing fry that closely resemble the adults. Consequently, ovoviviparous species have fewer eggs and larger fry than oviparous species. The most common ovoviviparous species are the poeciliids (e.g., guppies and swordtails), but the coelecanth also practices this reproductive method.

Viviparous

Viviparous reproduction is similar to ovoviviparous reproduction, but in the former method, there is a placental or blood connection between the mother and the eggs. Thus, the developing embryo acquires the necessary nutrients and oxygen from its mother. Once the developing embryo reaches full term, it is born alive. Viviparous species generally produce the smallest number of fry, but they typically are much larger than both oviparous and ovoviviparous fry. The most common viviparous species are sharks, but this form of reproduction also is found in the highland live-bearers of the family Goodeidae and the surfperches of the family Embiotocidae.

Reproductive strategies

Each reproductive mode, in combination with habitat, physiology, and behavior, plays an important role in the overall reproductive strategy. A reproductive strategy may dictate a large quantity of small eggs and high mortality or fewer large eggs with a greater chance of survival. These strategies must be designed such that a percentage of the eggs will survive through sheer numbers, camouflage, parental care, or retention in the maternal or paternal body. In addition, time and location are important with respect to supplying ample food for the young and access to space occupied by the adults.

Gametogenesis

Gametogenesis refers to the origin and development of mature gametes through the processes of spermatogenesis and oogenesis.

Spermatogenesis

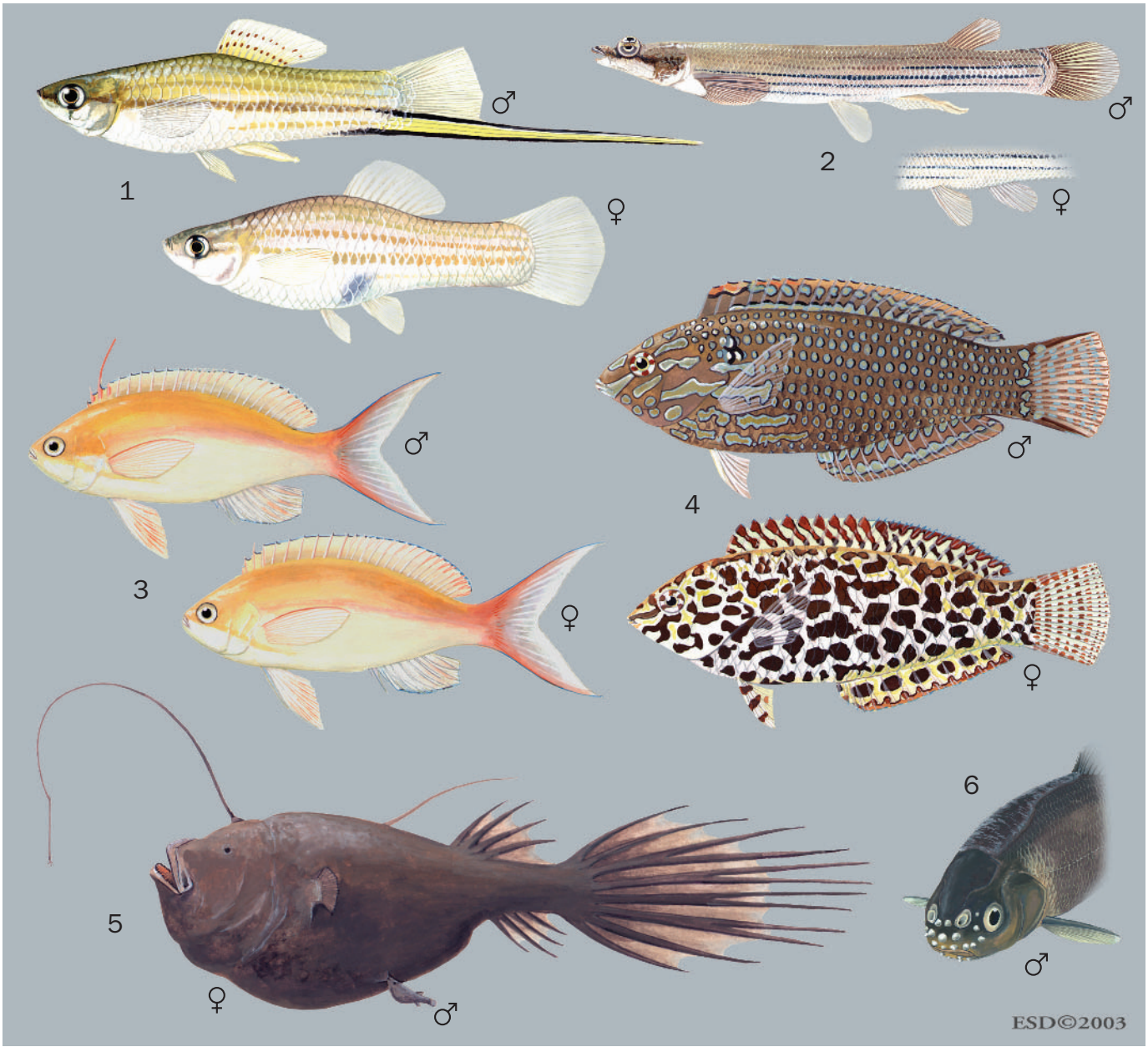
Spermatogenesis is the process in which spermatozoa are produced by follicles in the paired testes that undergo a series of meiotic and developmental transformations. Although spermatozoa consist of three parts (head, midpiece, and flagellum), they can differ between species. Despite the presence of the flagellum (tail), spermatozoa remain relatively inactive until they are released from the testes. At the time of spawning, the spermatozoa are combined with specialized secretions from the sperm duct (seminal fluid) to produce milt, which is released into the water during external fertilization. In the case of internal fertilization, the spermatozoa are transferred in packets called spermatophores. When combined with seminal fluid, the spermatozoa become very active. The life span of spermatozoa varies between species, and many other factors, such as temperature, have a profound effect. Spermatozoa remain viable for longer periods of time at lower temperatures. In addition, spermatozoa typically live longer when deposited inside the female compared with being exposed to the surrounding water. Long-term sperm storage and delayed fertilization of the eggs are characteristic of the reproductive biology of many ovoviviparous and viviparous fishes.

Oogenesis

The process in which ova (eggs) are produced in the paired ovaries is oogenesis. During oogenesis nutritional reserves are formed in the egg in the form of yolk material and oil droplets. The yolk is a source of protein, while the oil droplets provide fat and aid in buoyancy. Eggs can vary considerably in size, shape, outer shell characteristics, buoyancy, and adhesion. For example, most pelagic eggs are buoyant, whereas many demersal eggs are adhesive. The adhesiveness of an egg may facilitate fertilization, prevent unfertilized eggs from washing downstream, and allow eggs to attach to plants or rocks rather than falling onto the soft substrate, where they may suffocate. Eggs usually are deposited over a specific period of time rather than all at once. In addition, not all eggs present in the ovaries are deposited during spawning. Those eggs that are not deposited are resorbed by the ovaries, and the proteins, fats, and minerals are reused by the female for maintenance, growth, or egg production. In cases where there are too many eggs to be resorbed completely by the ovaries, the opening to the oviduct may become plugged with tissue, and the female becomes "egg bound." The obstructed oviduct prevents eggs from exiting the ovary during future spawning. In extreme cases, females that are severely egg bound may die.

Fecundity

The total number of eggs produced (fecundity) by a female may vary from one to two in some sharks to several hundred million in the ocean sunfish (*Mola mola*). In general,

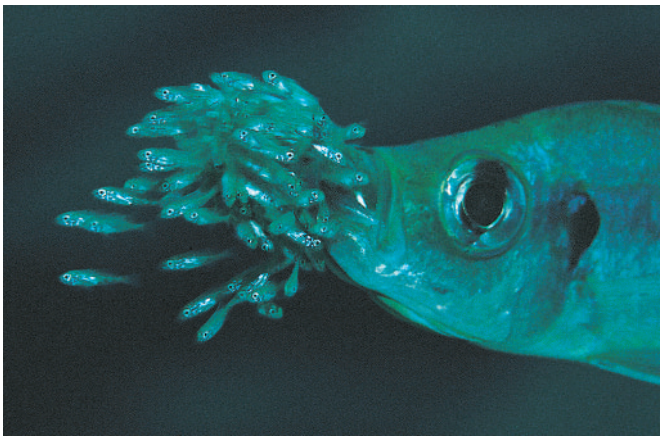


Examples of sexual dimorphism in fishes: 1. Swordtail, *Xiphophorus hellerii,* male has elongate lower caudal fin; 2. Largescale foureyes, *Anableps anableps,* male has modified anal fin (gonopodium); 3. Bicolor anthias, *Pseudanthias bicolor,* male has elongated dorsal spine; 4. Blackspotted wrasse, *Macropharyngodon meleagris,* different coloration and pattern; 5. Krøyer's deep sea anglerfish, *Ceratias holboelli,* parasitic male dwarfed by large female; 6. Fathead minnow, *Pimephales promelas*, male has breeding tubercles on its head. (Illustration by Emily Damstra)

fecundity declines with increasing egg size and parental care but increases with body size. In addition, fecundity is affected by numerous factors, including the species; age, size, and overall health of the female; food availability; time of year; and water temperature and quality.

Fertilization

In the vast majority of fishes, fertilization takes place outside the female's body. External fertilization may consist of varied types of spawning behavior, including paired or group broadcast spawning and oral fertilization. On the other hand, some fishes have internal fertilization. Males of those species that are involved in internal fertilization possess an intromittent organ, which is used for transferring the spermatophores. For example, in male sharks and poecilids, the pelvic and anal fins are modified into claspers and a gonopodium, respectively. Regardless of where fertilization takes place, fertilization is the point in time when a spermatozoa penetrates the chorion through a specialized opening called the micropyle. Once a spermatozoa enters the micropyle, the chorion hardens through a process known as water hardening, to prevent



A mouth brooding cichlid (*Haplotaxodon*) releasing fry in Lake Tanganyika, Africa. (Photo by Animals Animals ©Deeble & Stone OSF. Reproduced by permission.)

more than one spermatozoa from entering (polyspermy) and to aid in protecting the developing embryo. Some species, such as sturgeons, have multiple micropyle; thus, polyspermy does occur. Micropyle characteristics (e.g., size and shape) as well as other external egg characteristics (e.g., filaments, adhesive stalks, and tendrils) are quite varied among fishes. Once the spermatozoa enters the egg and the pronuclei and egg fuse, a zygote is created.

Embryology

Embryo development (embryogenesis) in fishes is similar to that of most vertebrates, with the embryo taking form on top of the yolk. Most teleost fishes, including elasmobranches and hagfishes, exhibit meroblastic cleavage, which involves cell division within a small disc-like region of the egg to produce the blastoderm (the disc of protoplasm where cleavage takes place) that eventually develops into a fish. On the other hand, lampreys have holoblastic cleavage, and bowfin, gar, and sturgeon have an intermediate form referred to as semiholoblastic cleavage. Holoblastic cleavage is total, resulting in equal-size blastomeres (cells resulting from cleavage). From this point of embryogenesis, cell division and differentiation continue in a prescribed manner, although the time at which specific structures appear varies among species. Before hatching, many structures and organs develop at least partially, including body somites (metameres or body segments), kidney ducts, the neural tube, optic and auditory vesicles, eye lens placodes (thickening of the epithelium), head and body melanophores, a heart and functioning circulatory system, pectoral and median fin folds, opercular covers, lateral line sense organs, and the notochord. At the time of hatching, the mouth and jaw may be barely formed, little if any ossification (bone formation) exists, fin rays may be present, and a nonfunctional gut and gas bladder are present.

At this advanced stage, the embryo is curled around on itself within the tight confines of the egg. Owing to the harsh and extreme environments (e.g., deserts and other arid environments) occupied by some fishes, they have evolved a reproductive strategy that involves a period of delayed development (diapause) for their embryos. For example, South American and African annual killifish fertilize and deposit their eggs in sand or peat moss in the rainy spring months. During the summer drought, when the pools of water dry up, the parent perishes, and the eggs enter a period of diapause. The rainy season of the following year triggers developmental completion and hatching.

The length of the developmental interval varies considerably, from a few days in surgeonfishes and several weeks in flatfishes up to several months in sharks. In general, the length of the developmental interval declines with increasing water temperature. When embryos are ready, hatching gland cells located on the head of some fishes secrete proteolytic enzymes, which breakdown proteins into simpler substances and aid in weakening the chorion. Erratic movements of the embryo's body and tail also aid in hatching.

Development

Larvae

Larval life generally begins when the young emerge from the egg and switch from internal yolk reserves to a diet consisting of plankton (e.g., diatoms, copepods, amphipods, ciliates, and larvaceans). The newly hatched, free-swimming individual, which may still have a large yolk sac attached, is referred to as a yolk-sac larva until the yolk is absorbed, after which it is referred to as a fry. At this point much larval development proceeds, including the axial skeleton, fins, organ systems, true and median fin rays and spines, scales, urostyle, hypural plate, and caudal rays. Characteristic pigmentation appears (including pigment in the eyes), and both the mouth and anus open and become functional. Before the development of the gill filaments, oxygen is absorbed across the membranous primordial fin folds through cutaneous respiration. The larval stage of fishes varies considerably in duration, ranging from one to two weeks in sardines (Clupeidae), about one month in many coral reef fishes, to several months or years in anguillid eels.

Egg cases containing lesser spotted dogfish (*Scyliorhinus canicula*) embryos. (Photo by Douglas P. Wilson: Frank Lane Picture Agency/Corbis. Reproduced by permission.)

Juveniles

The transition from larva to juvenile in many species (e.g., coral reef fishes) is associated with a change in habitat as juveniles settle out of the water column and take on a benthic, or reef, existence. In general, the juvenile phase is thought to begin when the larval characters are lost and the axial skeleton, organ systems, pigmentation, squamation (arrangement of scales), and fins become fully developed. It is at this time that the young take on the appearance of the adults. This transition in many species is very simple and can be completed in a short time (minutes to hours), as exhibited by damselfishes. This transition, however, is much more complex in some fishes and may involve significant alterations in the anatomy, physiology, or behavior of the species (e.g., metamorphosis in flatfishes and smoltification in salmon). In some fishes (e.g., Atheriniformes and Cyprinodontiformes) the immobile larval stage is bypassed, and the newly hatched fry are fully mobile and immediately capable of feeding actively.

Adults

By definition, an adult is a fully grown, sexually mature individual. Not surprisingly, the growth rate and age and size at which maturation occurs vary considerably in fishes. For example, the males of some surfperches are born with functional sperm, while it may take as long as 20 years for other fishes (e.g., sturgeon and some sharks) to mature. The spiny dogfish, which may have a life span of up to 70 years, may not become sexually mature until the age of 20 years. Among teleosts, American eels may not become sexually mature until they are 40 years old, at which time they participate in the spawning migration to the Sargasso Sea.

Senescence

In general, larger fishes live longer than smaller fishes, but the longevity of fishes varies considerably. Fishes that have a short life span (perhaps one year) include the South American and African annual killifishes as well as some North American minnows (*Pimephales* species), a silverside (Atherinidae), a stickleback (Gasterosteidae), and some gobies. Some of the oldest (90–140 years) fishes, whose ages have been determined through radioisotopic and otolith analyses, are scorpaenids from the northeastern Pacific. For the majority of all fishes, death is attributed to predation, accident, pathogens, accumulation of somatic mutations that cause a decline in health, alteration or loss of habitat, or commercial harvest. Among some fishes, death is attributed to senescence (old age), which refers to age-related changes in the body that have adverse effects on the organism. Over time these metabolic and anatomic processes make the organism more susceptible to death.

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Jeffrey C. Howe, MS

Freshwater ecology

Diversity of freshwater fishes

Only a small portion (0.01%) of the surface water of the earth is freshwater, but these areas represent a variety of habitats, including swift-moving streams, deep glacial lakes, and ephemeral creeks. These freshwater habitats harbor diverse assemblages of fish, comprising more than 10,000 species in 23 orders. Much of this species richness is represented by Cypriniformes (2,662 species), Characiformes (1,343 species), Siluriformes (2,287 species), and Perciformes (2,185 species). The Amazon River alone is home to more than 1,300 species of freshwater fish, and more than 700 species of endemic haplochromine cichlids inhabit the East African rift lakes.

Distribution of freshwater fishes

On global and regional scales, the distribution of freshwater fishes is determined largely by historical circumstances. The world can be divided into distinct zoogeographic regions based on the distribution of organisms around the globe. Patterns noted at the global scale have been influenced over a long evolutionary time period by plate tectonics, including the movements and collisions of continental landmasses (continental drift). Major tectonic events played a large role in determining the families of fish that are present on a particular continent and that have the opportunity to become part of local fish assemblages. The isolation of fish caused by the separation of landmasses allowed for the diversification of species within major lineages.

Continental movements also affected climate, geologic, and drainage patterns across the landscape. The latitudinal location of landmasses influenced their susceptibility to glaciation during cooler periods of geologic history. During the Pleistocene epoch (11,000 to 1.8 million years ago), four major glacial periods resulted in the extirpation of fishes in areas covered by ice sheets, caused other species to move to nonglaciated refugia, and altered large-scale drainage patterns. These effects still influence the distribution of fish today, as many species no longer inhabit certain areas or are recolonizing portions of their previous range after seeking southern refugia during the Pleistocene.

Geologically, mountains that are pushed up from the collision of two landmasses can restrict the movement of fish. For example, fish assemblages on one side of the Appalachian Mountains are substantially different from those on the other side of the divide. Mountains and other geologic features typically form the boundaries of drainage basins; the evolution of fish that are isolated in distinct drainages leads to further diversification and variance within species over time. Within drainage basins, a number of factors are associated with patterns of fish diversity. Fewer species tend to occur in headwater streams, while more species inhabit downstream portions of the watershed. The size and variety of local habitat types also affect fish diversity, with the diversity of fish increasing with habitat area and internal variability. In addition to natural controls on the range and composition of fish communities, it is important to recognize that human activities, including deforestation, construction of dams, introduction of non-native species, and pollution, have influenced the distribution of fish in many regions of the world throughout the course of recent history.

Acting within this broader context, physical and chemical characteristics of the environment regulate the composition and diversity of fish species that inhabit freshwater habitats. In all aquatic systems, light penetration and water temperature determine physical conditions that fish encounter. Fish also must be adapted to tolerate chemical attributes of freshwater systems, such as salinity, oxygen, and pH. Local species assemblages and species distribution within a habitat largely reflect the preferences of fish for different physical and chemical conditions.

Light

Light penetration directly and indirectly influences fish in freshwater habitats by warming the water, driving photosynthesis, and enabling visual activities. When light reaches the water surface, a small amount is reflected, and the remainder is absorbed as it enters the water column. Wavelengths of light are absorbed differentially with depth. Clear water in the upper few meters of the water column absorbs red wavelengths and converts the energy to heat. Only wavelengths between 400 and 700 nanometers can be used for photosynthesis, and these wavelengths penetrate deeper into the water column before they are absorbed. Light absorption is affected by particles and dissolved material in the water as well; for example, the presence of algae shifts absorption toward the green wavelengths. Light also enables fish to use vision to detect predators, prey, potential mates, and features of their habitat.

Temperature

Freshwater fish are ectotherms, and their internal temperature follows that of the surrounding water. Fish partition habitat space based on thermal gradients to avoid harmful temperatures as well as to take advantage of those that are optimal for a variety of physiological functions, including feeding, growth, and reproduction. Thus, seasonal movements and spawning are regulated strongly by temperature. Temperature varies on a geologic timescale, and shifts in the geographic distribution of fishes have been associated with major historical climatic changes. Temperature also varies locally and over short timescales, including diel and seasonal cycles, in freshwater aquatic systems. As light energy is converted to heat, the top portion of the water column warms first and to the greatest extent. Finally, latitude, altitude, and the velocity of water influence temperature. Due to large differences in water velocity, temperature patterns differ markedly in lakes versus running waters.

Salinity

Although rivers erode and transport some salts from geologic formations within the watershed, most bodies of freshwater lack the high concentration of dissolved salts that characterizes seawater. Exceptions occur in some desert areas of the southwestern United States and northern Mexico as well as in the Rift Valley of East Africa. In these areas, minerals accumulate when streams flow through underlying geologic salt formations or when evaporation leaves behind high concentrations of salts. While diverse fish communities inhabit these mineral-rich waters, most freshwater fishes cannot adapt physiologically to life in saline waters. Regulating internal salt concentrations poses a challenge to most fishes living in freshwater environments. Because salts are more concentrated inside their bodies than in the water, osmotic and diffusion processes work to bring in water and remove salts. To counter this situation, freshwater teleosts excrete large quantities of dilute urine and transport salts back into their blood using chloride cells. While this adaptation enables fish to osmoregulate in freshwater, the internal retention of salts also stresses most freshwater fish if they are exposed to saline conditions.

Oxygen

The concentration of oxygen in freshwater has serious implications for fish presence and distribution in a given area, and anoxia can result in the death of individuals. Oxygen enters water via diffusion from air at the water surface. Turbulence increases the surface area of water, such that moving waters contain more oxygen than stagnant waters. In addition, photosynthesis of plants, respiration of plants and animals, and the oxidation of organic materials drive diel changes in oxygen concentrations. Oxygen solubility in water is correlated negatively with water temperatures, and higher temperatures reduce dissolved oxygen levels. At the same time, fish metabolic rates and oxygen consumption levels increase with temperature, such that low oxygen conditions in warm water are particularly stressful for fish. To survive in low-oxygen waters, more than 40 genera of fish possess some capacity to breathe oxygen from the air; most of these species live in tropical freshwater habitats, where high temperatures and high rates of decomposition reduce the dissolved oxygen in the water.

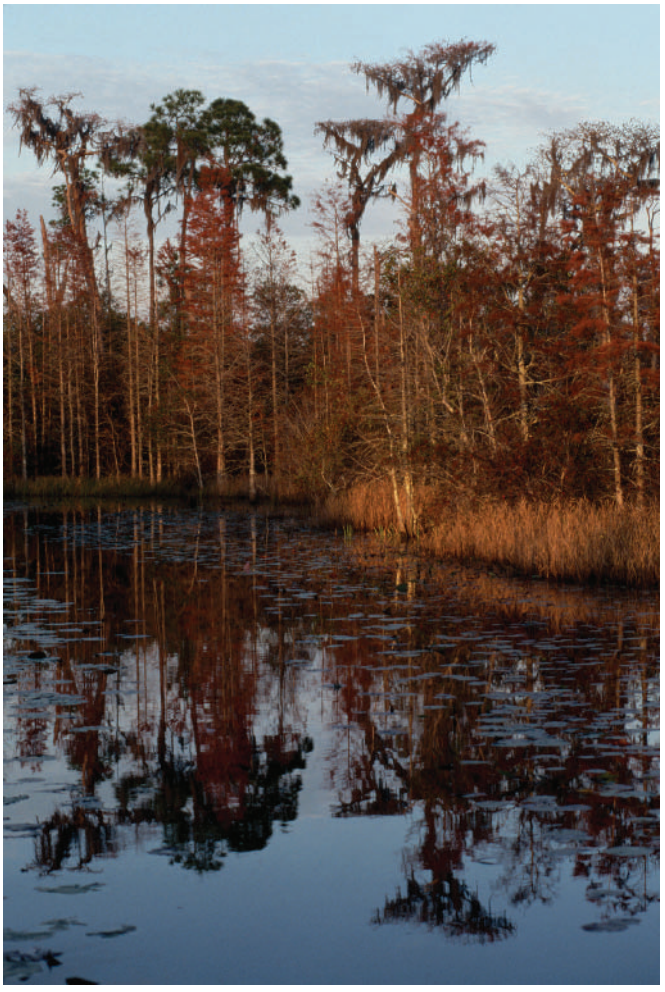
Tumultuous waters provide a very different environment for fishes compared to slow moving rivers. (Photo by Royalty-Free/Corbis. Reproduced by permission.)

pH

The relative acidity or alkalinity of a water body is measured as its pH. Hydrogen ions, which increase the acidity of water, are produced when carbonic acid dissociates from dissolved carbon dioxide in the water or from rainfall. The free hydrogen ions can be neutralized by carbonate minerals and buffered by calcareous compounds in geologic features surrounding bodies of freshwater. In poorly buffered systems, photosynthesis also can remove hydrogen ions and increase the pH of the water body. Metabolic functions of fish require pH within a certain range, and most fish cannot tolerate pH levels outside a range of approximately 4.0–10.0. High or low pH can be detrimental to reproductive success, gill function, and oxygen transport. Acidic pH appears to be most deleterious to fish. Acidic water dissolves metals, such as aluminum, that can be toxic to fish. In addition, the abundance and diversity of species, particularly of invertebrates that are eaten by freshwater fish, decline as water becomes acidic.

Major freshwater habitats

The variety of niches created by variation in physical and chemical factors within freshwater environments contributes to the great diversity of freshwater fishes. Many of these specific niches are organized within several major freshwater habitats. Most freshwater fishes inhabit streams, rivers, and lakes. Some fish prefer areas of swift-moving water in high mountain streams, others live at deep depths in lakes, and still others thrive in stagnant ponds.



The environment that fishes inhabit varies from the calm, slow waters of some rivers to the turbulant rapids of others. (Photo by Raymond Gehman/Corbis. Reproduced by permission.)

Lakes

Lakes are standing bodies of water surrounded by land, with small outflows relative to their internal volume. Lakes form in a variety of ways, including tectonic movements, volcanic activity, and glacial action. They also may originate as portions of rivers or bays that are cut off from the adjacent water body over time by deposition or sediment movement. Lakes receive inputs of water from the drainage basin, precipitation, and groundwater. These inputs are balanced by outflows of water to rivers, evaporation, and seepage into groundwater. The largest freshwater lake in the world is Lake Superior, which covers a surface area of 31,700 sq mi (82,103 km^2). Lake Baikal holds the largest volume of freshwater—14,292 cu mi (23,000 km^3). The 20 largest lakes contain over 67% of the total water in lakes worldwide, indicating that most lakes are small and shallow.

Ecological processes in many lakes are influenced greatly by a vertical temperature gradient that develops as sunlight warms the upper portion of the water column. Surface water warms when incoming radiation is absorbed and converted to heat. In temperate lakes the top portion of the water column heats during the summer, but temperature declines with depth. The warm surface water and cold bottom water are separated by the thermocline, a transition zone at the depth of greatest temperature change. Because water is most dense at 39.2°F (4°C) and becomes lighter by either cooling or heating, vertical temperature gradients and patterns of stratification vary with seasons and latitude. In cool portions of the temperate zone, differences in water temperature are minimal as the surface water of a lake warms to 39.2°F (4°C) in the spring; at this time, the lake mixes from surface to bottom. As warming continues, the lake stratifies in the summer, with a warm surface layer and cool deep waters. When the lake cools in the fall, stratification again breaks down. Reverse stratification occurs in the winter, however, as ice forms; colder, less dense water under the ice is suspended over warmer, more dense water around 39.2°F (4°C). The temperature gradient and stratification in lakes varies with latitude. In warmer temperate areas, the reverse stratification in winter does not occur, since ice rarely forms at these latitudes.

While it is common in temperate regions, this seasonal pattern of stratification driven by temperatures is not seen in all lakes. Some crater lakes may never stratify, because geothermal activity warms the deepest waters and minimizes temperature differences within the water column. Most tropical lakes stratify and mix on a daily basis. Annual variation in solar energy is minimal in the tropics, and daily changes in air temperature can establish and break down water column stratification. Wind is another factor that strongly affects stratification of many tropical lakes; wind adds kinetic energy to the lake and increases heat loss in surface waters. Some shallow tropical lakes, such as Lake Victoria, mix once a year when temperatures are lowest and winds are most persistent. Other deep tropical lakes may remain permanently stratified. For example, Lake Tanganyika reaches a depth of 4,823 ft (1,470 m), but the kinetic energy from wind cannot mix the waters below 820–984 ft (250–300 m). Polar or high-altitude lakes also may be stratified permanently if they remain frozen throughout the year.

Stratification of lakes caused by temperature gradients has two major effects on biological components of the lake ecosystem. First, stratification restricts mixing of nutrients within the lake to the area above the thermocline, unless wind or another turbulent force physically disturbs the lake waters. Thus, nutrients and other organic materials that enter the lake cannot be used to support production after they sink below the thermocline. Primary productivity of the lake is enhanced when vertical stratification breaks down. Spring blooms of plankton are common because sunlight for photosynthesis and nutrients from bottom depths are both available. In addition to affecting primary productivity, stratification can lead to oxygen depletion below the mixed zone, which affects the vertical distribution of many aquatic species. Oxygen is supplied in lakes by exchange with the atmosphere or from photosynthesis of green plants, both of which occur only in the upper portion of the water column. Organic matter eventually sinks to deeper waters below the photic and mixed zones, where it consumes oxygen through respiration and decomposition. The extent of oxygen deple-

tion is greatest in highly productive lakes that are stratified for long periods of time.

Although abiotic factors establish the physical and chemical template of habitat conditions in lakes, biotic components and interactions also structure the ecology of lakes. Primary producers, such as phytoplankton, algae, and plants, form the basis of the food chain in lakes. As explained earlier, however, primary productivity follows seasonal patterns based on the availability of light and nutrients in the water column. Zooplankton graze on phytoplankton, but much biomass from primary producers eventually settles to the lake bottom, where it provides food for benthic detritivores, including insects, oligochaetes, and mollusks. Predation by fish has a strong effect on food webs in lakes. Although fish fill a wide variety of feeding niches, many species of fish, particularly as juveniles, consume large quantities of zooplankton. Pelagic fishes in lakes are typically strong swimmers that capture crustaceans and insects as the dominant component of their food supply, while others are predatory piscivores.

Rivers and streams

Rivers and streams flow downhill in defined channels from headwater streams to main river channels to estuaries. The Nile is the longest river in the world—4,180 mi (6,727 km). The Amazon drains the largest area (nearly 2.3 million sq mi, or 6.0 million km^2) and carries the greatest flow, with a total discharge at its mouth of 6.4 million cu ft per second (180,000 m^3 per second).

The nature of streams and rivers is determined largely by their setting in the watershed. The drainage basin is the total area drained by a river system, including all of its headwaters and tributaries, and the number of fish species typically increases directly with the area of the drainage basin. Streams within the drainage basin can be classified at tributary junctions to determine their stream order, a measure that serves as a useful indicator of stream size, discharge, and drainage area. As stream size increases, so does the order; thus, the smallest streams are termed "first order," and the confluence of two first-order streams is identified as a "second-order" stream. The process continues toward the main river channel until it has been assigned the appropriate order. Each increase in stream order represents three to four times fewer streams, each of which is roughly twice as long and drains approximately five times the area of a stream of the next smaller order.

Streams and rivers are considered physically open systems, meaning that physical factors, such as width, depth, velocity, and temperature, change continually along their course from source to mouth. The "river continuum concept" emphasizes the continuity of the structure and function of river communities from headwaters to lowland portions of river channels. This concept uses stream order as its basis and suggests that changes in physical conditions, functional feeding groups, and species diversity occur dynamically and continuously along the gradient from upstream to downstream portions of rivers.

The discharge of water increases from headwaters to the main stem of rivers and determines the size and habitat features of the channels. Low-order streams tend to flow alternately through riffles, pools, and runs. Riffles are shallow, high-gradient stretches where fast-moving water flows over rocky substrates and creates turbulence. Pools are deep, low-gradient areas through which water moves slowly. In runs, water flows rapidly but smoothly. Slopes decrease in higher-order streams and rivers, such that they flow smoothly through their channels. River channels meander along a sinuous course. At each meander, the river deposits materials on the inward portion of the curve, where velocity is slowest, but high water velocities erode the outer portion of the curve. Velocity also affects the type of substrate and presence of vegetation in particular areas of flowing waters. For example, large particles, such as gravel, are transported only by fast-moving water. Finer particles, such as sand and silt, form the substrate in areas where current is slower.

Rainbow trout (*Oncorhynchus mykiss*) are transferred from holding ponds through a tube into a fish stocking truck at the Leaburg Fish Hatchery before being placed in the McKenzie River, in Leaburg, Oregon. (Photograph. AP/Wide World Photos. Reproduced by permission.)

Biotic patterns in streams and rivers are heavily influenced by the outcomes of physical processes. Many species of fish require specific substrates for spawning, while other substrate types and flow patterns support aquatic vegetation. Vegetation and woody debris are important to freshwater

fish as well; both offer cover from predators, spawning areas, and food-rich foraging sites. In addition, as discharge varies with seasons and precipitation, rivers may overflow their channels and flood riparian wetlands or floodplains, temporarily expanding the vegetated habitats available to freshwater fish. In the tropics, where precipitation primarily occurs during one or two rainy seasons throughout the year, numerous fish communities are dependent on these seasonal floods to expand available habitats, increase feeding opportunities, and mobilize nutrients within the river.

In temperate regions, primary production is necessary as the basis of the food chain in streams and rivers, and algae attached to the sediment surface are the predominant primary producers. Some fish, such as loaches (Homalopteridae) and catfishes (Loricariidae), consume algae directly by scraping it off rocks in the stream. More commonly, aquatic insects and crustaceans are relied upon as intermediaries between the algae and fish—invertebrates graze on algae in small streams, and fish feed on the aquatic invertebrates. As the stream gradient decreases, mosses, rooted plants, and filamentous algae become important primary producers upon which invertebrates and fishes feed. Detritus also may constitute a major part of the food chain, particularly in streams or rivers with extensive cover of streamside vegetation. Scavenging invertebrates and fish feed on the organic detritus. In medium-size to large rivers, members of the fish fauna engage in diverse feeding strategies, including herbivory, invertebrate feeding, piscivory, omnivory, and detritivory.

While primary production from within the system forms the energy base in temperate streams, the large diversity of fish species and productivity exhibited in tropical streams is supported by organic matter from outside the system. Tropical streams and rivers generally flow through dense forested areas. Although large streams may be wide and open to the sun, small streams may be shaded completely by the forest canopy. Instead of relying on photosynthesis as an energy source, life in these streams depends on organic matter that enters in the form of leaves or detritus from the forest. The warm water of these tropical streams enhances colonization by bacteria and fungi, which break down the terrestrial organic matter. Some fish consume the detritus directly, but most species rely on decapod crustaceans and, to a lesser extent, insects as intermediate detritivores. In larger streams, fish are dependent on energy that enters during the rainy season. Rains produce an increase in suspended organic particles and terrestrial insects that are washed from the land into streams. The most important energy sources become available to fish inhabiting tropical rivers when the river floods adjacent areas of land. Fish then can exploit food resources in the form of decaying vegetation, seeds, fruits, and insects that are available on the floodplain.

Other freshwater habitats

Although streams, rivers, and lakes provide the most abundant and important habitats, fish inhabit other bodies of freshwater as well. As mentioned briefly earlier, such wetlands as river floodplain marshes, shoreline marshes along lakes, and deepwater swamps provide an expanded foraging and refuge area for fish when they become inundated with water. Wetlands are particularly important as nursery habitats for a variety of fish species. Fish also utilize extreme habitats, such as underground caves and desert streams. Unique adaptations enable fish to survive in these environments. Many fish in caves have reduced eyes, and some are blind; instead of relying on vision, enhanced chemosensory and tactile abilities allow them to locate food, mates, and living space. In ephemeral streams, fish survive periods without water by resting in mud or another substrate during the dry season, depositing eggs that do not hatch until water inundates the streambeds in the following year, and utilizing respiratory adaptations to breathe atmospheric oxygen.

Interconnections of freshwater habitats

While physical, chemical, and biological features of different freshwater habitats have been distinguished here, it is important to recognize that all aquatic habitats truly are interconnected. Rivers flow into and out of lakes, rivers and lakes may spill over into wetlands, and rivers and streams may even flow through underground caves in the midst of a surface route. These linkages form a continuum of habitats that often extends to estuarine or marine systems. In addition to these physical connections, biotic connections are important among freshwater habitats. Organisms may disperse between habitat types directly or via a vector. Furthermore, sustaining a food web in one habitat may be dependent on nutrient inputs from another portion of the aquatic system or from terrestrial uplands. Because of the high level of interconnections between aquatic habitats, an action that is detrimental to one component may prove harmful to a much larger system. Recognizing these interconnections is essential for understanding the ramifications of human activities on aquatic environments.

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Marine ecology

Introduction

The ecology of marine fishes is a broad topic that may be addressed only in general terms here. The important factors for consideration are few, however. Quite simply, fishes interact with their physical environment; with other organisms, such as plants, invertebrates, reptiles, and mammals; and with other fishes. How and why these interactions occur is the focus of this discussion. In particular, we focus on aspects of the following: community ecology, population ecology, life history and reproductive ecology, habitat use, special habitats and adaptations, and feeding ecology.

Communities, assemblages, guilds, and niches

A community consists of all the organisms present and interacting within a given area. For example, a coral reef community consists of corals, benthic algae, phytoplankton, zooplankton (both demersal and pelagic), various micro- and macro-invertebrates, fishes, reptiles, marine birds, and marine mammals. There are numerous links, in terms of both habitat and trophic relationships, between members of each group.

Fishes and other organisms occur in assemblages within a community. A fish assemblage is composed of all the species populations within the community. Assemblages have order and structure, and both are maintained by interactions between species within the assemblage and with assemblages of other kinds of organisms within the community.

Within an assemblage are groups or species of fishes with similar patterns of resource use. These are called guilds. Although many guilds may consist of members that are taxonomically related to one another, membership is determined by ecological factors. For example, a guild of obligate *Pocillopora eydouxi* coral-dwelling fish species could include one or more hawkfishes (*Neocirrhites armatus*, *Paracirrhites arcatus*, and *Paracirrhites forsteri*—Cirrhitidae), a coral croucher (*Caracanthus maculatus*—Caracanthidae), a scorpionfish (*Sebastapistes cyanostigma*—Scorpaenidae), a goby (*Paragobiodon* species—Gobiidae), and a damselfish (*Dascyllus reticulatus*—Pomacentridae). In this example, only the hawkfishes are closely related to one another, although this relationship is not necessary for guild membership. Another example of a guild would be all those species that browse benthic algae, pluck zooplankton from the water column, or hide beneath the sand. Furthermore, juveniles and adults of the same species might not be members of the same guild. For example, juveniles of numerous species may shelter in mangrove roots, but as adults some of those species are found living in association with corals.

The place a fish has within the community or assemblage is its niche. A niche simply defines habitat, microhabitat, and physical parameters within the two, as well as diet and feeding strategies, symbiotic relationships (if any), and other functional roles (i.e., its role in predator-prey interactions). Thus, within the guild of obligate coral-dwelling fishes described earlier, we would find coral crouchers living deep within the branches of the coral and feeding upon coral-dwelling microcrustaceans or passing zooplankton, while in another niche, the larger freckled hawkfish, *Paracirrhites forsteri*, would be perched on the outer branches of the same coral and ambushing smaller fishes or crustaceans that passed close by.

Considerable debate has taken place over the way in which fish assemblages, particularly those of reef fishes, are ordered and structured. This debate is centered on questions of how highly diverse assemblages are maintained, how so many species can coexist, what limits diversity and abundance, whether composition and structure is temporally and spatially predictable, and whether the processes involved are uniform across geographical scales. Essentially, assemblage structure was thought to be the outcome of deterministic or stochastic processes. Deterministic processes emphasize fine-scale ecological niches that encompass interactions, such as competition, cooperation, predator-prey, and so on between species. Larvae settling onto a given site of the reef would recruit successfully and become established only in the absence of conspecific adults in favored niches or in vacant niches otherwise. Stochastic processes are random, in that successful recruitment is dependent on chance. Actually, both kinds of processes operate on assemblage structure, and their relative importance is felt on different temporal and spatial scales.

Population ecology

Population structure is dependent upon rates of reproduction and survivorship among individuals within the pop-

ulation. Population structure is also influenced by rates of migration into and out of the population. Recruitment of larvae, both locally produced and from distant sources, is another major factor. One hypothesis about the effects of recruitment on population size and structure is the recruitment-limitation hypothesis. In this case, the number of adults per unit area is limited by the number of larvae available for recruitment. (This hypothesis also has been proposed to explain assemblage structure.) The rates of these various factors vary annually, and the overall structure of a given population may be denoted by year classes (ages) or cohorts. Some year classes are stronger or larger than others. This difference has implications for the management of populations under exploitation by fisheries, because if the largest or most successful year class of a given population reaches maximum age and subsequent year classes are not so successful, overfishing occurs, and the population could be in danger of collapsing.

With some species, age structure also may reflect size structure within a population. Thus, a population of a species with indeterminate growth may consist of different-sized fishes at different levels of abundance for each size class. In the case of many reef fishes, however, size becomes a poor indicator of age, because growth tapers off after a few years or less, depending on the species and certain environmental factors. Growth rates of individuals within populations determine how much biomass is produced for a given population during a given unit of time.

Natural mortality affects population structure too. Starvation; disease; predation on eggs, larvae, juveniles, and adults; cannibalism; and old age all contribute to natural mortality. Mortality caused by fishing is additive, and total mortality for any given population under exploitation is a matter of concern for fisheries and conservation managers.

The genetic structure of marine fish populations is determined by gene flow within and between populations of the same species. Interpopulation gene flow is dependent upon the level of connectivity between two populations. Populations that are relatively close together geographically and served by the same current regime are more likely to have higher levels of gene flow compared with distant populations. In contrast, isolated populations are more likely to diverge over time. Geographic or ecological variation in characters may result. If this variation is great and reproductive isolation occurs, speciation (the creation of new species) may ensue.

Competition exists if two or more fishes require the same resource and the abundance of that resource is limiting within a given area. Competition between fishes of the same species is termed "intraspecific," whereas competition between different species of fishes or between a fish and another organism, such as a sea urchin, using the same algal resource, is deemed "interspecific." Intraspecific competition is an important factor contributing to the success of one individual over another within a population of the same species. This success may be measured ultimately by the proportional reproductive contribution to the population that one individual makes. Interspecific competition is important for determining the structure, and hence diversity, of an assemblage of fishes.

This coral reef is near Townsville, Queensland, Australia. More than a quarter of the world's coral reefs have been destroyed by pollution and global warming and unless drastic measures are taken, scientists warn that most of the remaining reefs may be dead in 20 years. (Photograph. AP/Wide World Photos. Reproduced by permission.)

The relative success of a population of one species over another at securing a vital resource, such as microhabitat or food, determines which species persists and which does not. If so, then how can many fish assemblages be so diverse? Usually, competition is reduced or avoided altogether by resource partitioning among species that live together in as state known as "sympatry." In our coral-dwelling fish example, we see that coral crouchers and hawkfishes avoid competition for the same coral and food resources by living in different parts of the coral and eating different kinds of food. An example of a situation wherein competition probably functions is the case of two fish species that have identical food or habitat requirements but live apart in spatially or geographically distinct areas in a state known as "allopatry." If two or more allopatric species with the same ecological requirements come together, there probably will be two outcomes. The first is that only one species will "win out" and continue to use the contested resource while the other(s) will fail to become established. The second is that all of the species in question will become established, because there will be a shift in resource utilization, sometimes quite dramatic and including rapid morphological changes relevant to the resources available, with only one species using the original resource while the others adapt to using different resources.

The interaction between predators and prey in a given assemblage affects prey in many ways but also may have implications for the population of predators. With respect to prey, predators can cause mortality or injury, with obvious negative consequences. Or the steady influence exerted on prey species by predators results in changes in the way prey utilize habitat or food resources so as to avoid predation. These changes have a profound effect on how the prey population reproduces and sustains itself.

The size of a population of prey species affects the ability of the predator to influence that population. Thus, the number of

Icebergs float in the Arctic Sea near the coast of Barrow, Alaska, USA. The changing climate in Alaska is causing sea ice to freeze later in the winter and break up sooner in the spring, which is changing the habitat of sea animals that live there. (Photograph. AP/Wide World Photos. Reproduced by permission.)

predators in a population may increase in direct proportion to an increase in the size of a prey population. This is an example of a density-dependent response that is compensatory; that is, the predator compensates for the increased number of prey by increasing its own numbers. If the prey population becomes too large and the predator population does not keep pace, the ability to influence the size of the prey population is reduced. In other words, there is safety in numbers. This form of density-dependent response by the prey population is depensatory, which is defined as a decrease in the relative risk of predation or impact upon the population by predation because of an increase in prey numbers.

What happens to the predator population when the prey population disappears? This is an intriguing question, especially with respect to coral reef systems that have been affected negatively by natural or anthropogenic (caused by man) habitat destruction. For example, groupers (Serranidae: Epinephelinae) like to feed on their cousins, the fairy basslets (Serranidae: Anthiinae). Fairy basslets tend to recruit, as post-larvae, to corals. If a coral bleaching episode kills off the corals on a given reef, the fairy basslets have nowhere to recruit. In time, the population of fairy basslets will decline, and there will be few or none left for the groupers to eat. Will the grouper population decline, or will its members simply switch to another kind of prey and get by? Conversely, what happens to the fairy basslet population if the grouper population is reduced greatly by overfishing? Will the fairy basslet population increase significantly in size, or will some other factor come into play? These are important questions that require further attention in the study of reef fish assemblage interactions.

Life history and reproductive ecology

Marine fishes, like their freshwater counterparts, possess a number of life history and reproductive traits and strategies that enable them to live and reproduce successfully under a variety of environmental conditions. These traits and strategies may vary geographically, historically, and hence phylogenetically within or between species. Many of the most important traits and strategies are discussed here.

Body size varies among marine fishes, with both the largest, the whale shark (*Rhincodon typus*, Rhincodontidae), and the smallest, a dimunitive goby (Gobiidae), existing in the same environment. Different body sizes confer distinct advantages. Large body size is favorable for species that swim in the water column. Large size conveys greater protection against predation by all except the largest predators and also allows for greater storage of energy and longer and faster swimming abilities. The latter comes at a cost to reproductive effort, however, because energy that would be available for reproductive activities is required instead for somatic (body) growth. Small body size, on the other hand, allows for greater access to benthic shelter and the potential utilization of a wider spectrum of food items, but at a greater risk of predation. Naturally, there are exceptions to these examples. Small-sized baitfishes, such as anchovies (Engraulidae) or reef herrings (Clupeidae), swim openly in the water column, whereas large-sized morays (Muraenidae) or wolf eels (Anarhichadidae) are associated closely with benthic shelter. Within species, larger body size conveys distinct advantages in terms of territory size, the acquisition of mates, and reproductive success.

Age and size at maturation in marine fishes also vary. Generally speaking, a marine fish that matures at an early age and at a smaller body size has a greater opportunity to reproduce before dying but usually has relatively low fecundity and smaller eggs. However, for pelagic spawning fishes, the acts of courtship and spawning expose the participants to predation risk from lurking predators. Also, energy diverted toward reproductive effort typically means that growth is slower in these fishes. In contrast, older and larger fishes invest in growth, delay reproduction, and have a greater risk of death before reproduction first occurs. On the upside, the larger female fish are more fecund and produce either more eggs or larger eggs; the larger male fish produce more sperm and, within species, may have more opportunities to mate compared with smaller fishes. The relationship between age and size in marine fishes has long been thought to be linear for most species. Recent studies of numerous reef fishes, however, have shown that growth in many species may be rapid at first but tapers off after a few years, yet these fishes may live for several more years. Thus, body size cannot be used to predict age in these fishes.

Sex ratios may vary both within and between species of marine fishes. One reason may be the population size within a given area, and another may be the age of those individuals that make up the population. The sex ratio is important in relation to effective mating opportunities and the development of a mating system. Marine fishes may be gonochoristic, in that the sex is determined genetically and they begin life either as a male or as a female. A variation on this theme is known as "environmental sex determination." In this case, the sex is determined by some environmental factor, such as seasonal water temperatures. Thus, females of a given species are produced during one time of year at a given temperature, whereas males are produced later in the season at a different temperature.

Marine fishes also may be hermaphroditic, in that they are capable of changing from one sex to another and, in some species, back again. Alternatively, they may function as both a female and a male either sequentially or simultaneously. Protogynous sex change occurs when a female changes her sex to become male. Males generally are larger than females in this system. Protandrous sex change takes place when a male changes his sex and becomes a female. In this case, females are larger than males. The former strategy is more common than the latter. Control of sex change is largely social in relation to mating system dynamics, but age also may be a factor in many species. A third variation has been described for some highly site-attached species, such as coral-dwelling gobies of the genus *Paragobiodon* (Gobiidae). Here, a larger female changes sex, becomes a male, and realizes greater fitness by spawning with smaller resident females. If, however, a larger male joins this new male, the new male will be forced to compete with the larger male for access to the resident females and probably will lose. Thus, it will forfeit mating opportunities as well. The sex-changed male will change sex again, reverting back to being a female, but will still realize some measure of fitness by staying on and spawning with the larger male.

Sequential hermaphroditism occurs in some species, such as the hamlets, *Hypolectus* (Serranidae), in that a mating pair switches sexual roles during long bouts of courtship and spawning. First, one fish spawns eggs that are fertilized by the second fish. Afterward, the second fish spawns eggs that are fertilized by the first fish. Simultaneous hermaphroditism occurs when an individual is capable of producing both eggs and sperm at the same time. This less common strategy is practiced largely by fishes that dwell in deep waters (such as many members of the order Aulopiformes), where the probability of encountering a mate is relatively low. Some species, such as numerous wrasses (Labridae) and parrotfishes (Scaridae), have a dual strategy, in that males and females are determined genetically (primary phase) but females can undergo protogynous sex change and become males (terminal phase).

The number of mating partners a fish has during the course of a breeding season is known as the "mating system." Generally, marine fishes are monogamous, polygamous, or promiscuous. Monogamy consists of a single pair that may join together only for spawning but also may share a common territory or home range and remain together for one or more seasons. Polygamy occurs in two principal forms, polygyny and polyandry. Polygynous groups vary in form. For instance, a single male mates with two or more females, and mating may occur in a socially controlled group. Alternatively, males may form leks with other males in a specific area for the purpose of displaying to and attracting several females for spawning. Males also may defend nests or spawning sites within fixed territories and mate with two or more females in succession. In polyandry, females mate with more than one male over the course of a season. For some species, such as anenomefishes (Pomacentridae), a single female in an anenome exerts control over and spawns with two or more resident males and, through social interaction, delays the growth and maturation of additional males that also may reside there. Promiscuity occurs when males and females spawn together, with little or no mate choice.

There is some plasticity in the mating system in relation to local population size. For example, if a population of the humphead wrasse (*Cheilinus undulatus*, Labridae) is relatively large at a given locality, it will form a polygynous spawning aggregation. If the population level is quite low, however, it may reproduce in a single-male polygynous mating group. Similarly, the obligate coral-dwelling longnose hawkfish, *Oxycirrhites typus* (Cirrhitidae), is polygynous if the coral in which it dwells is large enough or near enough to neighboring corals to support a male plus two or more females. If the coral is capable of supporting only the male and one female, the pair is facultatively monogamous.

Sexual dimorphism in size or color pattern usually is found in polygamous and, to a lesser extent, some promiscuous species but seldom in monogamous species. Larger size or more distinct color patterns confer advantages for attracting mates and maintaining relationships with them. Regardless of the mating system used by a given species, if mates of one species are difficult to find, an individual may choose to spawn with a closely related species that is more common, and hybrids might result. Typically, these hybrids do not produce viable offspring should they have an opportunity to mate.

Marine fishes spawn eggs with external fertilization, lay eggs after internal fertilization, or have internal fertilization with the release of fully developed young. There are at least four different modes of spawning and external fertilization. Demersal spawning includes the deposition and fertilization of eggs in nests or directly on the substrate; in pouches, such as those of male pipefishes and seahorses (Syngnathidae); or by oral brooding, such as in cardinalfishes (Apogonidae), in which the eggs are deposited and cared for within the mouth cavity of a parent. Pelagic spawning is the release of eggs and their subsequent fertilization at the peak of an ascent into the water column by a pair or spawning group. Numerous species of marine fishes spawn in this manner. Fishes that spawn pelagically in the water column but have eggs that sink to the bottom are known as egg-scatters. On the other hand, fishes that spawn pelagic eggs close to the bottom are known as benthic egg broadcasts. In contrast, some species, such as skates (Rajidae), are oviparous and have internal fertilization but deposit egg cases that develop and hatch externally. Live bearers have internal fertilization of eggs, and then the eggs develop inside the mother before the young are released. There are two forms of this trait. When eggs develop with nutrients contained in the yolk sac but without nourishment from the mother, it is called "ovoviviparity." Stingrays (Dasyatidae), for example, have this reproductive trait. "Viviparity" is when the young receive nourishment from the mother during their development. An example would be the tiger shark (*Galeocerdo cuvier*, Carcharhinidae).

The timing of spawning or breeding also varies; it may occur at dawn, dusk, during daylight, or at night. Factors include light level, tidal state, mating system, and reproductive mode. Spawning or breeding frequency and seasonal duration vary within species, because of local environmental conditions, and between species, because of phylogenetic differences. Frequency of spawning or breeding is controlled by physiological and phylogenetic constraints that limit the production of eggs or the ability to brood young. Other factors include lunar periodicity and access to mates. Seasonality is highly pronounced and is dependent upon annual variation in water temperature, the number of hours of daylight, and a host of other factors. On tropical reefs, where temperatures are generally warm and stable throughout the year, some hawkfishes (Cirrhitidae) court and spawn daily all year long. The same species at higher latitudes are limited to spawning only during warmer months. Groupers (Serranidae) that form spawning aggregations in the tropics or warm temperate regions, on the other hand, may spawn only once or twice a year in relation to lunar phase. Fishes living in cold temperate regions may be limited to spawning only when there is a shift in season, such as from winter to spring or summer to autumn, whereas others spawn strictly during the warmer summer months. Whether spawning or breeding frequency and seasonality favor adults or their progeny is a subject of considerable interest.

Fecundity or clutch size varies with species, body size, egg size, age, spawning frequency within a season, and latitude in relation to both the length of the season and the water temperature. Generally, there is a positive relationship between body size and egg number. Larger fishes produce more eggs compared with smaller fishes. The relationship is not always so neat, however. Because fecundity can be partitioned into three kinds—batch, seasonal, or lifetime—it is possible for smaller fishes to have relatively greater fecundity than larger fishes. For example, a smaller fish that spawns one or more batches of eggs per night for the course of a spawning season that could last all year in the tropics might have greater fecundity seasonally or over the course of its lifetime than a larger fish that spawns just once during a relatively short season and then dies.

Egg and larval sizes vary between species and also may vary within species, depending on body size, latitude, or other geographical or environmental factors. Generally speaking, large eggs mean that a greater amount of resources has been devoted to their production, and the result is large larvae, better equipped for survival. The advantage of smaller eggs is that more can be produced per unit time compared with larger eggs, and thus there are more opportunities to produce viable young. The drawback to small egg size is that, with fewer resources made available for development, the larvae also will be small and less equipped for survival.

Parental care in fishes includes the investment a parent makes before spawning or breeding, or prezygotic parental care, and the investment made after spawning or breeding, or postzygotic care. An example of the former strategy is nest building, while the latter includes nest guarding, oral incubation, pouch brooding, or internal brooding. Postzygotic parental care of eggs and larvae is practiced extensively by freshwater fishes but far less so by marine fishes. Among marine fishes, postzygotic parental care of eggs means that small, cheaply produced eggs could be afforded a benefit that increases their chance of survival. Ironically, most species that practice parental care in the marine environment tend to have eggs that are much larger than those produced by species that lack parental care. Pelagic spawning, egg scattering, and benthic broadcast spawning are practiced by a majority of marine species, and they do not engage in parental care.

The duration of time between egg fertilization and hatching varies with egg size. Small eggs spawned pelagically usually hatch rapidly compared with larger eggs that require tending. Similarly, eggs fertilized internally require a longer gestation time before the young emerge from the mother. As most marine species have pelagic larvae, the amount of time spent drifting passively or swimming weakly in the water column varies with species and also with environmental circumstances. Larval life duration depends on the growth rate of the larvae, which in turn is dependent upon its energy stores, rate of metabolism, and ability to feed before settling. Rapid growth to a larger size dictates that energy requirements and metabolism will be high, and thus the need to feed more often will be greater, or else starvation will occur, and death will result. Exposure to predation also is greater, and most larvae fall victim to predators or the effects of starvation before settlement takes place. Small larvae with short larval life durations and poor dispersal capabilities are more likely to settle and recruit locally. Short larval life duration means less risk from predation, because rapid settlement into favorable habitats can be accomplished. If settlement does not occur and the larvae are

carried out to sea, however, they, too, will die from predation or starvation. Size and the growth rate potential do not always influence dispersal capabilities of larvae, however. Larvae of many tropical reef species, for instance, may be adapted to long larval life and hence possess long-distance dispersal capabilities. These same larvae, however, may be caught or trapped by local oceanographic conditions and disperse only short distances before settling into suitable habitats.

Lifetime reproductive effort typically is defined in two ways. Fishes are either semelparous or iteroparous. Semelparous species usually reproduce only once in a lifetime, with a spawning event that may be quite large, depending upon the species. Examples include the freshwater eels (Anguillidae) and various salmons (Salmonidae), although some individuals of the latter group may survive and return to spawn again. Iteroparous species spawn or breed frequently during their lives, either in the course of a single season or over many seasons, depending upon the species. Examples include groupers (Serranidae), hawkfishes (Cirrhitidae), or parrotfishes (Scaridae).

Habitat use

Marine fishes live virtually everywhere in the world's oceans. In general, marine fishes may be found at the upper limit of the intertidal zone down to the bathypelagic realm several thousand meters deep, from freshwater in the upper portions of an estuary system to the hypersaline waters of now landlocked bodies of water or shallow flats in arid regions, and from balmy tropical reefs to intensely cold polar seas. Their distribution in these diverse habitats is made possible by behavioral, anatomical, and physiological adaptations that meet the specific or unique demands of those habitats. The classification of habitats is complex and is the subject of considerable interest if not outright debate. This review adopts a simple approach and considers habitat in relation to patterns of zonation based on depth and substrate.

Marine fishes that live on the bottom or in association with some form of structure on the bottom, such as a rock or submerged mangrove root, are considered to be benthic or demersal species. Those that swim up into the water column, whether in a shallow estuary or bay, in the open ocean, or in the deep open ocean, are considered to be pelagic species. Some species are both, in that they live in close association with the bottom but frequently are found in the water column, either foraging or moving over a wider area away from shelter. These species are considered to be benthopelagic species. With respect to depth, these kinds of fishes can be found across a wide range.

Among benthic fishes, certain species are specialized to live—as juveniles, adults, or both—in shallow tide pools or splash zones at depths of less than 1.5 ft, or 0.5 m. Examples of tide-pool fishes include certain morays (Muraenidae), marine sculpins (Cottidae), blennies (Blenniidae), and gobies (Gobiidae) that shelter within the confines of the pool and may endure the effects of a falling tide. The clingfishes (Gobiesocidae) are well adapted to life in both tide pools and the splash zone above them. Their ventral fins, modified into effective sucking discs, allow them to cling to stone walls above tide pools that are immersed only by the splash of waves. Some clingfishes, and indeed other tide-pool species, are especially well adapted to avoid desiccation and thermal extremes. Benthopelagic fishes in tide pools, such as damselfishes (Pomacentridae) or kuhlias (Kuhliidae), swim about in the depths of the tide pool. Generally, these kinds of fishes are less tolerant of the effects of low water levels or temperature shifts and must migrate out of the tide pool with the falling tide, only to return again as the tide floods.

Tidal effects also are pronounced in estuaries, mangroves, sea-grass flats, algal and shallow kelp beds, coral reef flats, and other kinds of flats dominated by mud, sand, rubble, cobble, larger rocks, or living organisms, such as oysters. In estuaries, benthopelagic and pelagic fishes move upstream with a flooding tide, often well into freshwater, and then move back downstream with a falling tide. These fishes are termed "euryhaline" species, in that they are tolerant of a wide range of salinities. Fishes living among mangrove roots, inshore seagrass flats, or algal beds, whether in or adjacent to an estuary, are adapted similarly. Benthopelagic and shallow pelagic species, such as halfbeaks (Hemirhamphidae) or mullets (Mugilidae), simply move off their various flats with the falling tide. Benthic species often seek shelter in holes, under rocks in depressions, and in deeper pools, or they may migrate to adjacent channels.

The effects of tide upon the fishes' habitats are less pronounced in the subtidal zone. Here, the various habitats are submerged constantly. Tidal effects typically are limited to patterns of current flow and what may be carried to and from this zone with the current. Thus, food, in the form of prey moving off a shallow flat in the intertidal zone with the falling tide, may be brought into the subtidal zone. Similarly, sediments from intertidal habitats move with the tide, creating turbid conditions in deeper water. Subtidal habitats are quite diverse as well and include coral and rocky reefs, sea grasses, algal and kelp beds, and deeper flats of sand, mud, rubble, rocks and boulders, and hard bottom or pavement. Some of these flats may be dominated by certain kinds of organisms, such as sponges, soft corals, or oysters.

Some habitats have pronounced levels of zonation as well. Coral reefs are a good example. Typically, there are three kinds of coral reefs: fringing reefs, where the reef is adjacent to a shoreline; barrier reefs, where the reef is well offshore and usually runs parallel to the adjacent landmass; and atolls, which are reefs that grow and emerge as a landmass, typically a sea mount, sinks beneath it over time. Barrier reefs and atolls usually have lagoons. Fringing reefs, being much narrower, have back troughs or some other form of channel on the reef flat within the intertidal zone. Regardless, seaward from the edge of the reef, one would find the reef front or spur-and-groove zone, one or more reef terraces or benches, and the reef slope. The reef front may be a shallow wall that drops directly from the reef margin to the first terrace. Fishes living here generally are pelagic or benthopelagic, although a number of benthic species may be found among emerging corals, in holes, or around rocks. Alternatively, the spur-and-groove zone extends outward from the reef margin in a pattern

resembling a human hand. The "fingers" of the hand represent spurs of coralline rock that extend outward from the face of the reef. Live corals resistant to the effects of wave action may grow upon these spurs. The spaces between the fingers represent the grooves, which are nothing more than surge channels between the spurs. These grooves are shallow at the reef face and deeper as the first terrace is approached, and the bottom of the channels consists of coral rock pavement, boulders, dead coral rubble, sand, or live corals.

Often, a complex network of holes, caves, and tunnels exists within this zone, with direct connections to the reef flat above. Elongated spur-and-groove zones, especially those that extend well out onto the deeper first terrace, are indicative of the effects of the rise and fall of sea levels historically. Numerous species of benthic, benthopelagic, and pelagic species are found in the spur-and-groove zone. For example, blennies and damselfishes utilize holes or corals on the spurs or in the grooves. Morays, lionfishes (Scorpaenidae), squirrelfishes and soldierfishes (Holocentridae), and sweepers (Pempheridae) employ the network of caves and tunnels within this zone. Certain hawkfishes (Cirrhitidae) or groupers (Serranidae) may perch on corals or hide on ledges or next to rocks and ambush passing prey. Reef herrings (Clupeidae) may swim in the water column above and flee the approach of predatory trevallys (Carangidae) that patrol this zone right to the reef margin.

Below the spur-and-groove zone is the reef terrace or bench; there may be one or more of these, depending on local geological history and changes in sea level. Coral development on the terrace, independent of geographic variation, is dependent upon the degree of exposure to wave action. In somewhat protected areas, the diversity and abundance of corals may be relatively high, whereas in areas exposed to heavy wave action and scouring, the diversity and abundance of corals may be low, and coral pavement predominates. Regardless, fishes in the terrace zone utilize what is available to provide shelter, food, and mating sites. Benthic fishes, such as damselfishes, hawkfishes, and scorpionfishes, make use of corals. Benthic species, such as sandperches (Pinguipedidae), blennies, and gobies, employ holes, sand-filled depressions, boulders, and pavement. Benthopelagic species, such as snappers (Lutjanidae), goatfishes (Mullidae), butterflyfishes (Chaetodontidae), angelfishes (Pomacanthidae), wrasses (Labridae), parrotfishes (Scaridae), and filefishes (Monacanthidae), move about home ranges or defend territories. Pelagic species, such as gray sharks (Carcharhinidae), trevallys, and barracudas (Sphyraenidae), patrol the terrace in search of prey.

Deep slope and wall habitats generally occur below the reef terrace. In some places, such as atolls, the transition between the spur-and-groove zone and the wall or deep slope occurs without the presence of a reef terrace. In other places, one or more terraces are present before the deep slope begins, and the slope may separate two terraces from each other. Wall and deep slope habitats often are characterized by the presence of various corals, sea fans and black corals, sponges, hydrozoans, and numerous other benthic invertebrates. These offer shelter and food to innumerable species of small, benthic fishes. The face of the wall or slope may be eroded with numerous holes and caves that provide shelter for many diurnal species, such as groupers and dottybacks (Pseudochromidae), and nocturnal fishes, such as bigeyes (Priacanthidae), soldierfishes, and squirrelfishes. Off the face of the wall or slope are found hovering fishes, such as certain butterflyfishes, angelfishes, damselfishes, and fairy basslets (Serranidae), that feed upon plankton in the water column.

In reef systems with lagoons, some of the same general habitat types may be present. At the back side of a barrier reef flat or in a pass connecting the outer reef with the lagoon, there often is a slope or wall that drops down into the depths of the lagoon. These habitats generally are protected, although they may be subject to intense tidal currents, may have a rich community of benthic invertebrates, and, correspondingly, support a wide variety of species. Damselfishes, butterflyfishes, angelfishes, wrasses, and triggerfishes (Balistidae) may hover in the water column but seek shelter in or along the wall or slope as necessary. As the slope gives way to sand or rubble, garden eels (Congridae), sanddivers (Trichonotidae), gobies, and peacock soles (Soleidae) are visible, but if threatened, they will rush into holes or bury themselves in the sand. Shallow portions of the lagoon often have patch reefs or coral bommies (large, isolated coral heads) that function effectively as islands in a sea of sand and rubble. These islands provide structure and, no matter how small, attract a remarkable number of species. Lagoons also may have seagrass beds in shallower areas and a corresponding suite of species, such as juvenile emperor fishes (Lethrinidae), snappers, goatfishes, and parrotfishes.

A temperate region analog of the coral reef is the kelp forest. Kelp is a marine plant that may grow as long as 65.6 ft (20 m). It provides a dense jungle that is utilized by numerous temperate species and, depending upon depth and proximity to kelp, may offer different microhabitats to members of the same fish family. As such, different species will be adapted to the surface, mid-reaches, and base of the kelp and to the water column surrounding it.

Among fishes, location is everything. The exact place where a fish lives is known as its "microhabitat." Fishes, especially small fishes, have remarkable plasticity in what they adapt to as a home. For example, scorpionfishes, coral croucher, hawkfishes, damselfishes, wrasses, gobies, and numerous other species live within or atop the branches of corals. Moray eels, jawfishes (Opistognathidae), blennies, and gobies, among others, inhabit holes. Other water column–dwelling species, such as some triggerfishes, seek shelter in holes as well. Some species, such as pipefishes (Syngnathidae) and clingfishes, are specialized for living in crinoids and sea urchins. Similarly, various seahorses, hawkfishes, and gobies are specialized for life on sea fans and black corals. Pipefishes, seahorses, some juvenile wrasses, and filefishes mimic the leaves of sea grasses or fleshy algae. Blennies and many other small benthic species have adapted to life in empty seashells and worm tubes. Clingfishes, gobies, blennies, and labrisomids (Labrisomidae) live in sponges. Even the sand serves as a distinctive microhabitat. Snake eels (Ophichthidae) burrow under the sand and seldom emerge, except at night. Stonefishes (Scorpaenidae) and stargazers (Uranoscopidae) lie buried beneath the sand and ambush passing prey. There are numerous other examples of

benthic fishes that utilize natural and man-made structures as microhabitats.

The pelagic zone is divided into different zones relative to depth as well. The epipelagic zone ranges from the surface down to a depth of 656 ft (200 m). Between 656 and 3,281 ft (200–1,000 m) is the mesopelagic zone, followed by the bathypelagic zone at 3,281–13,123 ft (1,000–4,000 m), the abyssal zone at 13,123–19,685 ft (4,000–6,000 m), and the hadal zone below 19,685 ft (6,000 m). Most pelagic fishes occur in the epipelagic (more than 1,000 species) and mesopelagic and bathypelagic zones (about 1,000 species combined).

The epipelagic zone is the limit at which photosynthesis takes place. Phytoplankton occur there and form the basis for a food chain that consists of consumers ranging from zooplankton to blue whales. Fishes of the epipelagic zone have bodies that are streamlined, to allow for greater speed in the pursuit of prey or the evasion of predators. Many epipelagic species, such as dolphinfishes (Coryphaenidae), tunas (Scombridae), and marlins (Istiophoridae), make seasonal migrations to feed and mate. Speed often is essential, and many species have independently evolved the ability known as countercurrent exchange, which effectively turns them into warm-blooded organisms. This trait, found in mackeral sharks and tunas, among others, is especially useful in cooler waters. Species associated more with inshore waters, such as striped bass (Moronidae) and bluefishes (Pomatomidae), also make seasonal migrations to track prey movements and to reproduce. Reef-associated species, such as trevallys and barracudas may migrate for spawning, but the distances traveled are far less.

Many epipelagic species are denoted by their silvery, bluish, or greenish blue body coloration, which makes them difficult to see in open water and thus decreases the risk of predation. This coloration also benefits predators, allowing them to approach prey fishes more easily. Large predators, such as marlins and many tunas, are more darkly colored, however, and dolphinfishes are among the most brightly colored species in the epipelagic zone. Some species of epipelagic fishes are especially adapted for life at the surface. Specializations may include enlarged pectoral and caudal fins that may be used to facilitate escape, modified snouts that allow for greater feeding efficiency on the surface, or enlarged eyes that promote detection of potential predators and prey at the water-air interface. Predators include the needlefishes (Belonidae), which are capable of sudden, powerful bursts of speed that allow them to jump repeatedly out of the water in pursuit of prey. Prey species have adapted to escape this pursuit. Halfbeaks and ballyhoos also may make repeated jumps to evade predators. Perhaps the most famous example of aerial evasion is that of the flyingfishes (Exocoetidae), whose modified pectoral fins resemble wings and whose modified caudal fin rudders are capable, when touching the surface of the water while the fish is airborne, of supplying additional thrust. Flyingfishes can travel up to 1,312 ft (400 m) in a single flight at a speed of more than 43.5 mi (70 km) per hour and can make flights repeatedly in succession. Pelagic fishes not particularly adapted for flight often seek shelter beneath flotsam, under jellyfishes, or attached to other larger fishes. The remoras (Echeneidae), which attach themselves to sharks, rays, billfishes, whales, and even ships, are able to hitchhike around the epipelagic zone more or less under the protection of their hosts.

Those zones below the epipelagic have confounding physical and biological factors, the effects of which escalate with depth. Increasing water pressure, decreasing water temperature, little or no light penetration, seemingly vast spatial distributions, and the patchy distribution of food resources all heavily influence which fishes live where and how. There is a remarkable diversity in species, however, and, because many of these factors have similar effects upon unrelated species, there is also a extraordinary similarity in characters that have evolved through convergent evolution. Fishes of these zones may be large (more than 6.6 ft, or 2 m) or small (less than 2 in, or 5 cm), yet they possess large or elongated mouths and dagger-like teeth for grabbing prey. Others have tubular eyes that augment the efficiency of light detection. Conversely, many species lack functional eyes entirely and rely upon other senses. Numerous species possess photophores (light-emitting organs) to attract both prey and mates. They also may have modified dorsal fin rays or chin barbels, often with photophores, that are used to attract prey. Many species have thin bones and specialized proteins that allow for gas regulation and neutral buoyancy in the absence of swim bladders. Fishes distributed in relatively shallow mesopelagic waters at higher latitudes often are found at greater depths in the tropics. This phenomenon, known as tropical submergence, allows these species to expand their geographical distribution while remaining in cooler and more comfortable water temperatures. Pelagic fishes of these zones also migrate, but the direction is more vertical than horizontal. At night many species rise hundreds, if not thousands of meters in depth, some to the surface, before returning downward during daylight hours. These vertical migrations usually track the movements of prey during a 24-hour cycle. Other fishes, especially such deep benthopelagic and benthic species as the tripodfishes (Ipnopidae), never make the migration and depend solely on what they encounter or what "rains" down upon them from the water column above.

Special habitats and adaptations

As indicated earlier, marine fishes are specially adapted to living in extreme environments. Deep-water pelagic and benthopelagic fishes, as illustrated earlier, are prime examples of adaptation to extremes. There are numerous shallow-water examples, too. Some marine fishes, such as the reef cuskfishes (Ophidiidae), have adapted to the dim world of tunnels and caves beneath the reef front or spur-and-groove zone but emerge at night to hunt small fishes and invertebrates. Polar fishes have adapted to extremely cold water temperatures that may fall below 32°F (0°C). (It is a curious trick of physics that saltwater does not freeze at this temperature.) For example, the icefishes (Nototheniidae and others in the suborder Notothenioidei) of Antarctica and the Southern Ocean have evolved a specialized protein that acts as an antifreeze that prevents these fishes from freezing. These species have evolved to fill various niches too. Some, such as *Trematomus nicolai*, are benthic, whereas others, such as *Trematomus loennbergii*, are

benthopelagic in deeper water; still others, such as *Pagothenia borchgrevinki*, are pelagic and swim and feed just beneath the ice.

Fishes also have adapted to aerial exposure. Examples include clingfishes and blennies in the upper reaches of the intertidal zone and mudskippers (Gobiidae) of the genus *Periophthalmus*, which retain water in their gill cavities and are capable of hopping and skipping across mud flats, rubble flats, and among the branches of mangroves. Marine fishes have adapted to hypersaline conditions as well. In arid regions, back bays, estuary sloughs, tide pools, and now-landlocked seas, all tend to have salinity levels far higher than that of seawater. Some species of fishes, such as clingfishes and gobies, have evolved mechanisms that allow them to regulate their osmotic pressure under these conditions. There is a limit, however. The landlocked Dead Sea in the Middle East, with a salinity in excess of 200 parts per thousand (ppt), versus an average of 36 ppt in seawater, is simply too salty for fishes to survive. Conversely, some seas, such as the Baltic in northern Europe, have such low salinity levels in some areas that such freshwater species as the pike *Esox lucius* (Esocidae) may coexist with euryhaline marine species.

Species that migrate between marine and freshwater, or vice versa, during both juvenile and adult phases of their respective life cycles have managed to conquer the problems associated with different salinity levels and osmotic regulation. For example, anadromous fishes, such as the salmons and sea trout (Salmonidae), live most of their adult lives in the ocean but migrate up a river or stream (often the one in which they were born) to spawn. Their juveniles live for part of their life cycle in freshwater before moving downstream and out to sea. (Some populations may become landlocked, however.) Catadromous fishes, such as freshwater eels (Anguilidae), live their adult lives in freshwater but migrate well out to sea to spawn and die. Their juveniles often return to their natal streams to begin their adult lives. Amphidromous fishes, such as some gobies (Gobiidae) and sleepers (Eleotridae), also live their adult lives in freshwater and spawn there as well. Their eggs and larvae are carried out to sea, however, and the post-larvae migrate back up stream, sometimes against formidable barriers, to begin their lives as adults. Other amphidromous species are born in saltwater but have young that migrate into freshwater to grow and then return to saltwater to grow more and to reproduce as adults.

Feeding ecology

Marine fishes have a wide range of diets and methods of feeding. They may be divided generally into herbivores, carnivores, detritivores, and omnivores. Herbivores are those that feed upon plants and plant materials. They do so by grazing or browsing upon benthic algae, sea grasses, or other plant life. Other herbivores may use specialized gill rakers to strain phytoplankton from the water column. Some species, especially certain damselfishes (Pomacentridae), act as farmers of the benthic algae they consume. For instance, they may kill a patch of coral that subsequently is used as a substrate for benthic algae to recruit upon. The farmer fishes then tend the algae, removing unwanted species and feeding upon desired ones, at the same time that they defend the algal patch against other herbivores. Other herbivores, such as parrotfishes (Scaridae), may simply bite off and crush corals in order to strain the symbiotic zooxanthellae algae resident within the coral polyp.

Carnivores feed upon a great variety of animals. Zooplanktivores strain or pluck zooplankton from the water column. Corallivores excise or pluck polyps from their coral skeletons; alternatively, they may crush the corals with strong teeth and strain the polyps through their gill rakers. During coral spawning season, numerous fish species, especially butterflyfishes (Chaetodontidae) and damselfishes, feed upon coral eggs as they float upward into the water column. Others may be specialized to pluck or nip the tips of anenomes, hydrozoans, or other coral-like organisms. Some fishes may be generalists when feeding upon invertebrates, but others are highly specialized for taking only certain kinds. Thus, some fishes specialize in microinvertebrates, such as diminutive worms, crabs, shrimps, or mollusks, whereas others target macroinvertebrates, such as squids, octopuses, lobsters, or large crabs.

Invertebrate prey may be benthic, such as clams, oysters, and tunicates, or they may be pelagic, such as squids and swimming shrimp. Prey may be sifted from sand or rubble, crushed, grabbed, bitten, or swallowed whole. Some fishes are able to feed on prey items that may be difficult, if not dangerous, to consume. Some triggerfishes (Balistidae) can bite and crush sea urchins bearing venomous spines without apparent damage to themselves. Similarly, the humphead wrasse (*Cheilinus undulatus*, Labridae) can feed on adult crown-of-thorns starfish without being damaged by this organism's strong, venom-tipped spines. Pelagic macroinvertebrates may include jellyfishes that are consumed by molas or ocean sunfishes (Molidae) as they drift in the water column. Prey also may reside out of water. For example, archerfishes (Toxotidae) are specialized for feeding upon insects by shooting a stream of water at them so as to knock them down from mangrove branches or other forms of structure; the fallen insect then is consumed on the surface.

Piscivores feed upon fishes exclusively, although many species also vary their diet by consuming invertebrates. These predators actively hunt, chase, herd, grasp, stun, club, shock, ambush, bite, or engulf other fishes. Various small species are specialized for feeding on fish scales or skin, either as juveniles or as adults. Others, such as cleanerfishes (certain Labridae, Gobiidae, Chaetodontidae, and so on), have evolved to remove ectoparasites or damaged tissue from "client" fishes that visit their cleaning stations. Still other species are specialized as parasites that feed upon host fishes. Host fish species include potential predators (e.g., sharks, moray eels, needlefishes, groupers, snappers) as well as numerous other species that are active during daylight hours (e.g., butterflyfishes, angelfishes, damselfishes, wrasses, parrotfishes). Larger fishes, especially sharks, may feed on floating sea birds, reptiles, and mammals in addition to fishes. Detritivores sift detritus from the bottom and strain it through their gill rakers. Omnivores eat both plant and animal material as adults. Many species of fishes undergo ontogenetic shifts in diet and feeding methods, meaning that their diet and feeding methods change with age and growth. Species that feed upon phyto-

plankton or zooplankton as juveniles may switch to fishes or large invertebrates as adults.

Through their trophic interactions, fishes have important direct and indirect effects upon the structure of the communities in which they live. They can influence, among other factors, rates of productivity and biomass turnover, nutrient cycling, sediment production, shifts in water quality, shifts in food web composition, or shifts in species composition and relative abundance within a given assemblage.

Resources

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Terry J. Donaldson, PhD

Distribution and biogeography

Biogeography

Biogeography is the study of the geographical distribution of plants (phytogeography) and animals (zoogeography). This science attempts to explain how distributions of organisms have come about. These explanations depend upon a thorough knowledge of the phylogeny of the group and the geological history of the region. Freshwater fishes are especially important in understanding distribution patterns, because they are tied to their river systems, which are surrounded by a land barrier, which in turn is surrounded by a saltwater barrier.

Fish distribution and salt tolerance

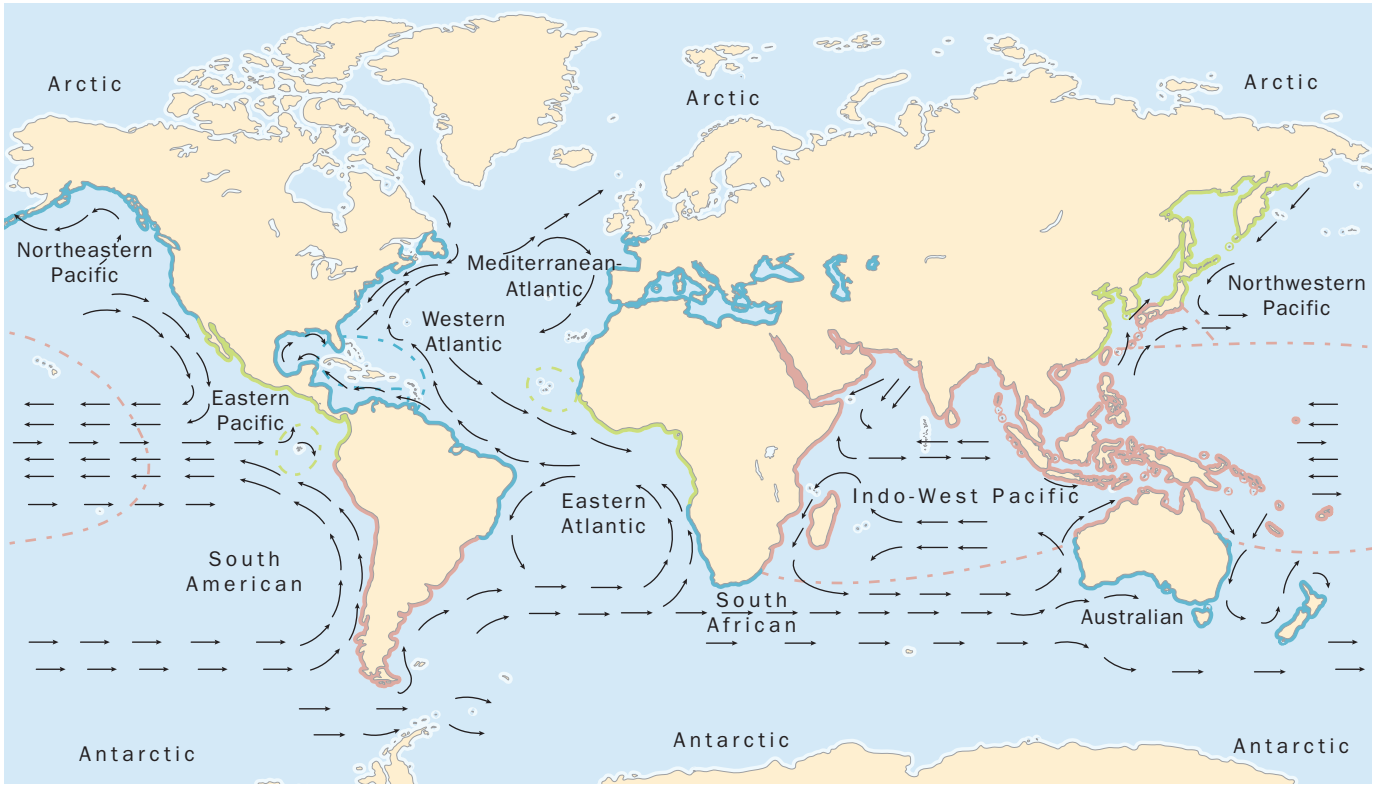
Fishes can be grouped into freshwater and saltwater families. Freshwater fishes can be subdivided into primary, secondary, and peripheral division families, depending upon their salt tolerance. The members of primary division freshwater fish families have little salt tolerance and are more or less restricted to freshwaters. Saltwater is a major obstacle for them, and their geographic distribution has not utilized dispersal through the sea. Such fishes include members of the minnow (Cyprinidae) and perch (Percidae) families. Fish families with some salt tolerance, whose distribution may reflect movement through coastal waters or across short distances of saltwater, are known as secondary division freshwater fishes. Examples of this group include the killifishes (Cyprinodontidae) and cichlids (Cichlidae). Peripheral division families derive from marine ancestors that used the oceans as dispersal routes. They have a wide range of salt tolerance. Some peripheral families spend part of their life cycle in freshwater (diadromous), whereas others are mostly marine but invade river mouths and may ascend into completely freshwater. The salmons (Salmonidae) and mullets (Mugilidae) are examples of peripheral division fishes. Many strictly saltwater fish families live only in the sea, but some may have a few species that occasionally enter brackish or freshwaters.

Habitat richness

Freshwater in lakes and rivers makes up less than one hundredth of one percent (0.0093%) of the total amount of water on Earth, whereas the oceans account for 97%. The remainder of the water is bound in ice, groundwater, atmospheric water, and so on. It is surprising that 42% of all fish species live in 0.01% of the world's water. This remarkably high percentage reflects the degree of isolation and the diversity of niches possible in the freshwater environment. The percentage of fish species in various habitats is as follows:

- Primary freshwater 33.1%
- Secondary freshwater 8.1%
- Diadromous 0.6%
- **Total freshwater 41.8%**
- Marine shallow warm 39.9%
- Marine shallow cold 5.6%
- Marine deep benthic 6.4%
- Marine deep pelagic 5.0%
- Epipelagic high seas 1.3%
- **Total marine 58.2%**

Stingrays swim in shallow waters near Grand Caymen Island. (Photo by Animals Animals ©James Watt. Reproduced by permission.)



Marine regions and ocean currents. (Map by XNR Productions. Courtesy of Gale.)

Marine fishes and zoogeography

The salinity of the world's oceans is about 35 parts salt to 1,000 parts water. This ratio varies slightly around enclosed, hot regions with high evaporation rates, such as the Red Sea, but for the most part, salinity is not a major barrier for marine fishes, except at the local level. Temperature, on the other hand, is a substantial barrier. The four major temperature zones of the ocean surface are tropical, warm temperate, cold temperate, and cold. Structure, in the form of continental shelves and coral reefs, also must be considered; ocean currents are obviously important; and the vast distances across open oceans are barriers to the dispersal of coastal species. The interaction of these factors and the geological history of a region affect the distribution of marine fishes. Fishes that live along the relatively warm shoreline and on the continental shelf down to about 656 ft (200 m) make up 39.9% of the world's fishes. This includes tropical, warm temperate, and cold temperate waters. If we consider that there are approximately 27,300 fish species, this means that about 11,000 fish species inhabit the shallow, warm to cold temperate water zone.

Marine shallow, warm waters

Tropical waters harbor the greatest diversity of fishes, most likely owing to the presence of coral reefs, which provide habitat, structure, and food. Reef-building corals need clear, clean water of at least 68°F (20°C). The faunal regions of the oceans have been delineated in different ways, and boundaries often are imprecise and overlapping. Most authorities agree, however, on the following system (or a similar one). These regions, which roughly correspond to Cohen's marine shallow, warm habitat, are the Indo-West Pacific, western Atlantic, eastern Pacific, eastern Atlantic, Mediterranean-Atlantic, northeastern Pacific, northwestern Pacific, South American, South African, and Australian. The remaining 18.3% of marine fishes are found in shallow, cold (Arctic and Antarctic), deep (cold), or epipelagic waters.

The Indo-West Pacific region extends from East Africa to northern Australia, southern Japan, and all of Polynesia. By virtue of its vast expanse, it has the richest fish fauna of any

Sheepshead minnows (*Cyprinodon variegatus*) are found in the salt marshes of New Jersey, USA. (Photo by Animals Animals ©Joe McDonald. Reproduced by permission.)

Geographic distribution of *Galaxias maculatus* and relevant ocean surface currents. (Map by XNR Productions. Courtesy of Gale.)

marine region, estimated to be about 3,000 species. The Indo-West Pacific also has more coral and other reef-associated invertebrate species than any other region. All of the tropical fish families found elsewhere are represented in this area, and most show their maximum diversity in the Indo-West Pacific region. Many species in this region have pelagic larvae and therefore are wide-ranging species. Springer linked the distribution of many species with the Pacific Plate, and Briggs divided the Indo-West Pacific into provinces defined by their degree of endemism, especially around isolated oceanic island groups, such as Hawaii. The East Indies Triangle (from the Malay Peninsula and Philippines through the Indo-Australian Archipelago to the Bismark Archipelago) is an important evolutionary center and contains the greatest species diversity in the marine world.

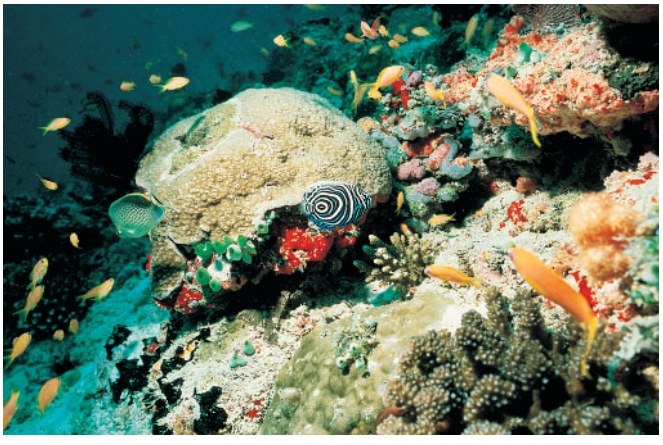
The western Atlantic region extends from the temperate coast of North America through the Gulf of Mexico and the Caribbean Sea south through the tropical and then temperate coast of South America. Parts of this region, especially the West Indies, contain coral reefs but only about one-tenth as many coral species as the Indo-West Pacific. There are approximately 1,200 fish species in the western Atlantic region. The warm waters of the Gulf Stream provide a connection for northern and southern elements of this region and probably have prevented the differentiation of the tropical fish fauna of the otherwise northerly Bermuda Islands. There is a decrease in the number of species along the western Atlantic coast as one moves north or south from the tropics into colder waters. Some authorities consider the northwestern Atlantic region from Cape Hatteras north to be a separate province.

The eastern Pacific region extends from the Gulf of California to northern Peru. The cold Peruvian Current that runs from the Antarctic up the west coast of South America abruptly ends the tropical conditions at the Gulf of Guayquil. The fish faunas of the western Atlantic and eastern Pacific are similar at the generic level, because they have been separated only recently by the elevation of the Isthmus of Panama about three million years ago. There are only a few coral species in the eastern Pacific, and the fish fauna likewise is much reduced from the numbers in the western Atlantic, with about 650 species. The Galápagos Islands fish fauna is relatively rich, with a large proportion of endemic species. A vast expanse of open ocean separates the extremely rich Indo-West Pacific fauna from the relatively depauperate eastern Pacific fauna. Only about 8% of the coastal species are shared between the central Pacific and the eastern Pacific.

The eastern Atlantic region is the smallest and least diverse of the four tropical inshore marine areas. This region runs along the West African continental shelf from Cape Verde to Angola. Coral reefs are nearly absent from this area. There are about 450 species of fishes, and roughly 25% of them are shared with the western Atlantic region. This may reflect a time when the South American and African coasts were much closer together. The region's remoteness probably accounts for the fact that approximately 40% of the species are endemic.

The warm temperate Mediterranean-Atlantic region is cooler than the inshore areas mentioned earlier. It includes the Atlantic and Mediterranean shoreline of Europe and Africa as well as the Black, Caspian, and Aral Seas. Northern and southern borders are ill defined, and warm waters of the Gulf Stream along the coast of Europe allow for a mixture of warm-water and cold-water species. There are about 680 species of fishes in the Mediterranean-Atlantic region, 540 of which are from the Mediterranean Sea, whose fauna is similar to the fauna of the Atlantic coasts of southern Europe and northern Africa.

The fish fauna of the northeastern Pacific region from Baja to the Aleutian Islands gradually changes from tropical to temperate to Arctic and is, therefore, very diverse. It is strongly influenced by the California Current, which brings cold water from the Gulf of Alaska down the California coast.



Coral reefs attract, feed, and house a large variety of fishes. (Photo by Animals Animals ©Mickey Gibson. Reproduced by permission.)

The northwestern Pacific or Asian-Pacific region extends from Hong Kong to north of the Kamchatka Peninsula. Its southern area overlaps with the Indo-West Pacific region. Temperate species reach their southern limit around Hong Kong, and the Bering Sea may be a barrier preventing exchange of coastal species between North America and Asia.

The South American region surrounds that continent from the coast of Peru around Tierra del Fuego and up the east coast to Rio de Janeiro. The borders are somewhat blurred, with tropical species in the north and Antarctic species in the south. The cold Peruvian Current and strong prevailing winds dominate the western coast of South America and produce upwellings of nutrient-rich waters that support large populations of anchoveta (*Engraulis ringens*) and other commercially important fishes as well as seabirds.

The South African region is warmer than the South American region, owing to its more northerly location and the warmer currents that surround Africa. Widespread tropical

Lungfish are able to survive when their pools dry up by burrowing into the mud and sealing themselves within a mucous-lined burrow. There are three genera surviving today and they are found in Africa, Australia, and South America. (Photo by Animals Animals © A. Root, OSF. Reproduced by permission.)

	Nearctic	Neotropical	Paleartic	Ethiopian	Oriental	Australian
# Primary Families	15	35	15	28	28	2
# Secondary Families	7	8	2	5	3	4
# Peripheral Families	9	8	13	3	11	14
TOTAL # FAMILIES	31	51	30	36	42	21
# Endemic Primary	8	32	0	17	14	1
# Endemic Secondary	1	2	1	1	0	2
# Endemic Peripheral	0	1	2	0	2	3
TOTAL ENDEMIC FAMILIES	9	35	3	18	16	7
% Endemic Primary	26	63	0	47	33	5
% Endemic Secondary	3	4	3	3	0	10
% Endemic Peripheral	0	2	7	0	5	14
% ENDEMIC TOTAL	29	69	10	50	38	33

Number of fish families and percent endemic in each biogeographical region, based upon 139 families. Widely distributed peripheral families are excluded. Data from Berra (2001). (Illustration by Argosy. Courtesy of Gale.)

The saber-toothed blenny (*Meiacanthus migrolineatus*) makes its home in a tubeworm off the coast of Egypt. (Photo by Animals Animals ©Mark Webster, OSF. Reproduced by permission.)

families dominate the fauna, and most of the cold-tolerant families typical of the South American region are absent.

The Australian region includes western, southern, and eastern Australia as well as New Zealand. The southern coast is home to temperate fauna, with some cold-tolerant species, whereas the tropical component increases as one moves northward as the result of the effects of the warm Pacific and Indian Oceans.

Marine shallow, cold waters

Arctic and Antarctic shore fishes down to 656 ft (200 m) make up about 5.6% of all fish species. The Arctic region extends from about 60° north into the Arctic Ocean, Bering Sea, and the waters around Greenland. It shares some species with the surrounding regions. The Antarctic region and Southern Ocean contain less than 300 species. Many of these are endemic species of notothenioids adapted to the extremely cold waters. The Antarctic shares very few species with surrounding regions, probably because the more temperate species did not survive as Antarctica drifted into its present position.

Marine deep waters

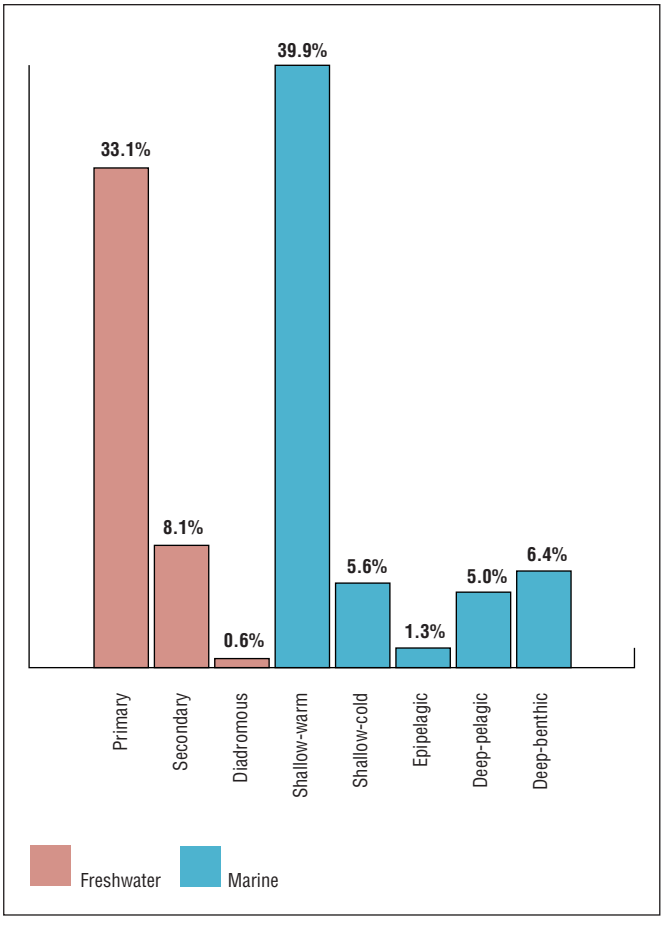
Deep benthic (bottom-dwelling) fishes are found below 656 ft (200 m) along the continental slope or on the deep-sea floor. These fishes constitute 6.4% of all fishes. Deep pelagic (free swimming in the open ocean) fishes, below 656 ft (200 m), make up 5% of all fishes. These fishes are not tied to continental shelves, and many have a worldwide distribution. The habitat of the deep open sea is relatively poor in nutrients and niches. Fish living from about 656 to 3,281 ft (200–1,000 m) are mesopelagic, and those dwelling deeper than 3,281 ft (1,000 m) in the water column are bathypelagic. Pelagic faunas can be divided into various regions, such as north and south, temperate, subtropical, tropical, Arctic, and Antarctic.

Epipelagic

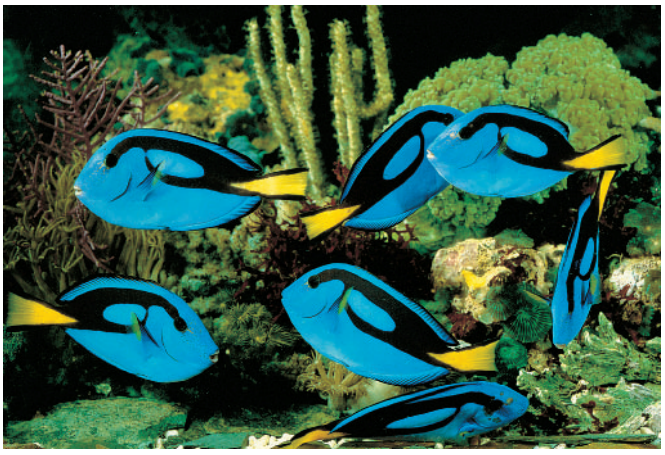
Fishes living from the surface to 656 ft (200 m) on the high seas are termed epipelagic. These are highly mobile fishes, such as the tunas, and many species are worldwide. Few niches are present in this habitat, and epipelagic fishes make up only 1.3% of the total fish fauna.

Freshwater fishes and zoogeographic realms

In his classic work *The Geographic Distribution of Animals*, published in 1876, Alfred R. Wallace recognized six major



Percentages of recent fish species living in various habitats. (Illustration by Argosy. Courtesy of Gale.)



The palette tang (*Paracanthurus hepatus*), as well as other colorful fishes, are found in the Pacific and Indian Oceans. (Photo by Animals Animals ©M. Gibbs, OSF. Reproduced by permission.)

zoogeographical realms: Neartic (North America, except tropical Mexico), Neotropical (South and Central America, including tropical Mexico), Paleartic (nontropical Eurasia and the north tip of Africa), Ethiopian (Africa and southern Arabia), Oriental (tropical Asia and nearby islands), and Australian (Australia, New Guinea, New Zealand, and Celebes and nearby small islands to the east). Wallace proposed a hypothetical boundary between the Oriental and Australian faunas. This line, which became known as Wallace's Line, passes between Bali and Lombok, between Borneo and the Celebes (Sulawesi) and south around the Philippines. It is not an exact boundary between the Oriental and Australian realms for all animal groups, but freshwater fishes, for whom saltwater is a barrier, have not crossed Wallace's Line to any significant degree. There is an important faunal break separating the depauperate Australian island fauna from the rich Oriental continental fauna. Of the 23 families of primary division freshwater fishes on Borneo, only the bonytongues (Osteoglossidae) have crossed Wallace's Line without the help of humans.

Freshwater distribution patterns

In the book *Freshwater Fish Distribution*, Berra analyzed the distributions of 139 families of primary, secondary, and peripheral division freshwater fishes. Each zoogeographic realm has its endemic families, which occur only in that particular region, and some regions are richer than others. The Neotropical realm has the most diverse fish fauna, with 51 families. Of these families, 32 (63%) are endemic primary division families, two are secondary, and one is peripheral. The 35 endemic families (69%) comprise river stingrays (Potamotrygonidae), South American lungfish (Lepidosirenidae), 13 families of characid-like fishes, 12 families of catfishes, six families of electric fishes, the Middle American killifishes (Profundulidae), and the foureyed fishes (Anablepidae).

The Oriental realm has 42 families, 14 (33%) of which are endemic primary division, none are secondary, and two are peripheral. The 16 endemic families (38%) include the Sundasalangidae, Gyrinocheilidae, seven families of catfishes, Indostomidae, Chaudhuriidae, Asian leaffishes (Nandidae), Pristolepidae, pikehead (Luciocephalidae), kissing gourami (Helostomatidae), and giant gouramies (Osphronemidae).

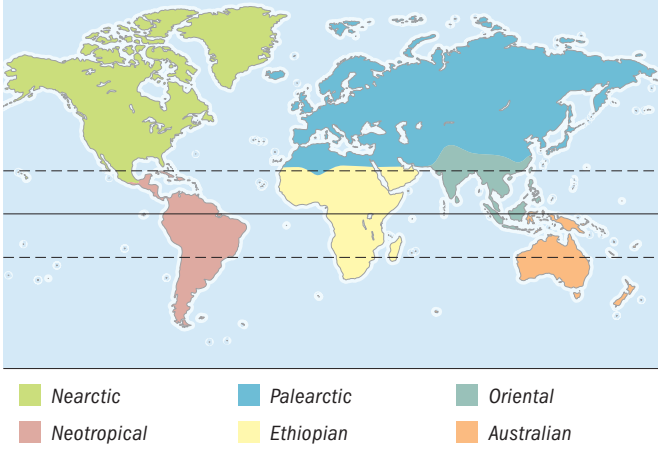
The Ethiopian realm includes 36 families, 17 (47%) of which are endemic primary division, and one is secondary. There are no peripheral endemic species. The 18 endemic families (50%) consist of African lungfishes (Protopteridae), bichirs (Polypteridae), butterflyfish (Pantodontidae), elephantfishes (Mormyridae), aba-aba (Gymnarchidae), denticle herring (Denticiptidae), Kneriidae, Phractolaemidae, four families of characid-like fishes, five families of catfishes, and Bedotiidae. For our purposes, Madagascar is considered part of this realm.

The Nearctic realm is home to 31 families, eight (26%) of which are endemic primary division, and one is secondary. No endemic peripheral division fishes are present. The nine endemic families (29%) include the bowfin (Amiidae), mooneyes (Hiodontidae), bullhead catfish (Ictaluridae), splitfins (Goodeidae), troutperch (Percopsidae), pirateperch (Aphredoderidae), cavefish (Amblyopsidae), sunfishes (Centrarchidae), and pygmy sunfishes (Elassomatidae).

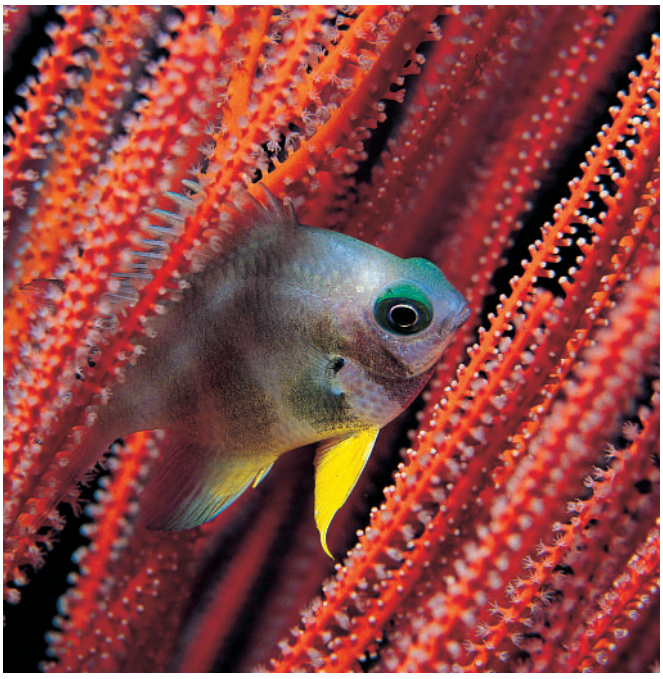
The Palearctic realm has 30 families, none of which are endemic primary division fishes. There are one endemic secondary and two endemic peripheral families. The three endemic families (10%) include the Valenciidae, Comephoridae, and Abyssocotidae.

The Australian realm has the fewest families in freshwater, with 21. Only one family is an endemic primary division, two are secondary, and three are peripheral; the division of one family is not certain. The seven endemic families (33%) are the Australian lungfish (Ceratodontidae), Australian smelts (Retropinnidae), salamanderfish (Lepidogalaxiidae), rainbowfishes (Melanotaeniidae), blue eyes (Pseudomugilidae), Celebes rainbowfishes (Telmatherinidae), and torrentfish (Cheimarrichthyidae). For our purposes, Sulawesi is considered part of the Australian realm.

The distribution of fishes within each biogeographic realm can be subdivided by drainage basin. These subdivisions are dis-



Freshwater fish families: the global pattern. (Map by XNR Productions. Courtesy of Gale.)



The shy damselfish peers out from swaying rods of soft coral of a Papua New Guinea reef. (Photo by Animals Animals ©Bob Cranston. Reproduced by permission.)

cussed by Banarescu, Bond, Moyle and Cech, Helfman et al., and Matthews. Berra summarized the biogeography of freshwater fish faunas and provided an entrance into the literature.

Families that occur in both the Nearctic and Palearctic regions are said to have a holarctic distribution. Examples include the sturgeons (Acipenseridae), pike (Esocidae), salmon and trout (Salmonidae), and perches (Percidae). The minnow family, Cyprinidae, is the largest fish family, with more than 2,000 species. It is the dominant fish family in the world's freshwaters, with a continuous distribution in Eurasia, Africa, and North America. It is absent from South America, where characiform fishes dominate, and it has not been able to penetrate the saltwater barrier surrounding Australia.

Continental drift

Between 1915 and 1936 Alfred Wegener published six editions of *The Origin of Continents and Oceans*, in which he proposed the idea that the continents originally were one large mass that subsequently fragmented, with the fragments drifting apart. He noted the congruence of the east coast of South America to the west coast of Africa and compared this pattern to a giant jigsaw puzzle. This idea met resistance until modern geophysical evidence of plate tectonics and paleomagnetics provided a mechanism for the way in which continents could move. About 200 million years ago all the continents were part of a huge landmass, Pangaea. This supercontinent began to fragment about 180 million years ago, resulting in a northern portion (Laurasia—North America and Eurasia) and a southern portion (Gondwana—South America, Africa, India, Antarctica, Australia, and New Zealand). Gondwana separated into the southern continents beginning about 90 million years ago and, propelled by convection currents in the earth's mantle generated by the heat of radioactivity, have been drifting into their present positions ever since. This, of course, has implications for the fish faunas carried on the continental plates, especially ancient groups such as the lungfish, which have families on three of the continents of Gondwana: South America, Africa, and Australia. Other more recent groups, such as the 18 families of characid-like fishes, show a South America–African connection. (Bond, Moyle and Cech, Helfman et al., Matthews, Lundberg, and Lundberg et al. comment on the relationship between continental drift and freshwater fish distribution.)

Dispersal

To understand the patterns of distribution, it is necessary to know the phylogeny and fossil record of the group under consideration as well as the geological history of the region. Lundberg provided an excellent analysis of South American–African fish distribution. In addition to vicariant events, such as drifting continents, freshwater fish also may disperse over a continent. Fishes may move from one drainage system into another during times of flooding. Stream capture due to lowland meanders or headwater piracy may provide access from one drainage system to another. Freshwater fish with some salt tolerance may swim through brackish water or saltwater from one river mouth to another and then ascend upstream. Streams may become connected by glacial meltwaters, thereby allowing passage of formerly isolated species. Some fish species, for example, walking catfish or eels, can wiggle through damp grass from one system to another. Mud attached to the feet of aquatic birds may contain fish eggs that hitch a ride to another drainage system. Waterspouts may pick up small fishes or their eggs and deposit them into another stream or lake. Lowered sea levels caused by glacial advance may isolate streams, or the elevation of a mountain range may divide river systems. This may lead to the divergence of initially similar faunas on both sides of a barrier. These are the sorts of factors that must be considered when trying to explain the distribution patterns of freshwater fishes.

Galaxias maculatus—a case study

The Southern Hemisphere peripheral division family Galaxiidae has a distribution that, at first glance, seems to reflect vicariance (continental drift). Most members of this family occur in Australia and New Zealand. Several species are in southern South America, however, and one species occurs at the southern tip of Africa. Whether vicariance or dispersal across the sea accounts for this pattern has been debated for decades. One species in this family, *Galaxias maculatus*, has received the most attention because it has one of the most extensive and disjunct distributions of any freshwater fish. It occurs in western and eastern Australia, New Zealand, Lord Howe Island, Chatham Island, southern Chile, Argentina, and the Falkland Islands. Berra has reviewed this "poster child" of vicariance versus dispersal.

The vicariance supporters suggested that because the galaxiids occur on all Gondwanan continents except India, their distribution reflects an ancient Pangaean pattern followed by continental drift. The dispersalists attributed the

wide geographic distribution to transoceanic dispersal of the marine larval stage, called "whitebait." It was suggested that *G. maculatus* originated in Australia and dispersed eastward past Tasmania to New Zealand and on to South America via the East Australian Current and the West Wind Drift. The dispersalists reasoned that if *G. maculatus* predates the breakup of Gondwana 65 million years ago, as the vicariance advocates suggest, there would be much greater differences between South American and Australian populations. Since these populations exhibit very few physical differences, they could not have been isolated for 65 million years. Proteins from muscle extracts of *G. maculatus* from western and eastern Australia, New Zealand, and Chile were used to test the hypothesis that populations from the western Pacific and the eastern Pacific do not differ genetically. Researchers found no fixation of alternative genes and only minor differentiation in gene frequency between western and eastern populations and concluded that the populations were part of the same gene pool, indicating that gene flow via dispersal through the sea is taking place. Using mitochondrial DNA variation, Waters and Burridge likewise supported the dispersal argument but reported greater population differentiation than was detected by Berra et al. with proteins. Waters et al. showed that intercontinental marine dispersal between New Zealand and Tasmania occurs but is insufficient to prevent mitochondrial DNA differentiation among continents.

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Behavior

Introduction

Fish behavior is often varied and complex within and between species. Sensory stimuli, cyclic influences, population density and structure, habitat quality, the availability and use of space, the potential for competition and coexistence, the need to avoid predators, foraging and diet, reproduction, and other factors all contribute towards the evolution of patterns of behavior and their use. Despite the great diversity of fish species, their wide patterns of geographical and spatial distribution, and their highly variable ecological requirements, there are a number of patterns of behavior common to all fishes, as well as unique adaptations that occur only in a few.

Sensory systems and behavior

The behavior of marine fishes is shaped by sensory information provided by any one of their senses, both singly and in combination. They use vision to detect prey, avoid predators, identify species, choose mates, communicate, engage in social and territorial interactions, select and use habitat, and navigate. Fishes use their inner ear to detect sounds made by conspecifics during communication, by approaching predators, or by other fishes as they feed. If the fish has a swim bladder, these sounds can be amplified. Low frequency sounds made by movement, including struggling, are detected by the lateral line. Fishes may communicate by rasping mouthparts, gill arches, or other organs, and amplifying the sounds with their swim bladders. Touch is important in prey detection, predator avoidance, social interactions, and courtship and spawning behavior. Olfaction (smell and taste) is important in many predators for the detection of prey. The barbels beneath the mouth of a goatfish are highly sensitive and allow this fish to taste, as well as feel, potential prey. The sense of taste also allows a fish to determine quickly where a prey item is palatable or toxic. Chemical cues are also utilized for navigation. For example, salmon utilize chemical cues to detect the natal stream, where they will return to reproduce and die. Some fishes, especially sharks, skates, and rays, and the electric freshwater fishes of the families Gymnotidae and Mormyridae, are capable of detecting minute electrical currents discharged by their prey. The patterns they detect allow them to pinpoint the location of the prey, even if lies buried under benthic sediments or is obscured by turbid or muddy water. Electroreception also allows some migrating fishes to determine their geographical position relative to Earth's magnetic field. Electricity is also used for communication in gymnotids, mormyrids, and some catfishes (Synodontidae and Ictaluridae).

Activity cycles

Fish behavior is influenced by various cycles that govern such activities as habitat use, feeding, migration, and reproduction. Circadian rhythms derived from internal or endogenous 24-hour clocks control hormone releases and subsequent behaviors. Changes in light levels on a daily or seasonal basis are a principle factor influencing rhythms. Lunar periods control tidal cycles that influence patterns of local migration, feeding, and reproduction. Seasonal shifts in water temperature or other climatic variables trigger migratory and reproductive behaviors.

Fishes and other organisms possess an internal, or endogenous, clock that is set to a period of approximately 24 hours for a given day. This clock can be adjusted daily by some sort of trigger or stimulus. Two common stimuli are the onset of daylight and the constant progression of low and high tides. The clock governs a number of basic behaviors, such as the onset of movement, feeding, or courtship, along with the hormonal activity that influences or triggers these behaviors.

Most freshwater and marine fishes are diurnal, or active in daylight, during a 24-hour period. As dusk approaches, diurnal species seek shelter in which to rest or sleep and are replaced by nocturnal species that are active during the night. At dawn, these fishes retire to shelter or simply rest until dusk approaches again. Some fishes ignore the changeover between day and night and are more or less active for 24 hours. The dawn and dusk changeover periods, also known as crepuscular periods, also trigger pronounced reproductive or predatory activities in a number of species. Vertical migrations, in which deep-dwelling species rise hundreds or even thousands of feet in the water column at night, only to descend when daylight approaches, are also triggered during these times.

Tidal shifts, either the onset of low tide or high tide, and the corresponding movement of water off or onto a flat, tide pool, or other type of habitat, govern the movements of fishes

within or between affected habitats. For example, as the tide falls in a tide pool, residents must move out of the pool and seek shelter elsewhere to avoid desiccation or thermal shock. As the tide returns, so do the fishes. Similarly, predators cue on the outgoing tide and move to locations where prey will gather or pass through as they move out of an affected habitat. Tidal shifts also trigger courtship and spawning behaviors that favor the movement of pelagic eggs and larvae off the reef or flat to avoid benthic predators or, alternately, to allow pelagic larvae to move back onto the reef or flat for settlement.

Temperate marine and freshwater fishes often spawn on a seasonal basis, usually during spring or summer, although others spawn in the autumn prior to the onset of winter. Spawning in spring or summer provides an opportunity for larvae to feed and grow before the falling temperatures of autumn and winter slow growth and activity rates. Fishes spawning in the autumn have eggs that may overwinter and hatch with the onset of spring. Spawning in river species is often timed to coincide with annual or seasonal flood cycles that trigger migrations, but that also provide feeding opportunities for juveniles and adults and the increased dispersal of young.

Tropical, and some temperate, species court and spawn in relation to phases of the moon. Some species are semilunar, in that they spawn every other week in relation to the new and full moon. Others are lunar, in that they spawn just once a month, either on the new or full moon. The actual day of spawning relative to moon phase may be variable, as a number of species spawn on the days on either side of the new or full moon, but reach a peak at a the height of the phase. Semilunar and lunar spawning may also be seasonal. For example, a number of groupers (Serranidae) form spawning aggregations once or twice a year, with the time of formation centered around a specific phase of the moon.

Many reef fishes, particularly those tropical species resident at low latitudes, court and spawn daily. Their reproductive cycle is regulated by daily shifts in light. Some species spawn at dawn, others at dusk or into the night, and still others during daylight, but the time of spawning shifts daily in relation to tidal phase.

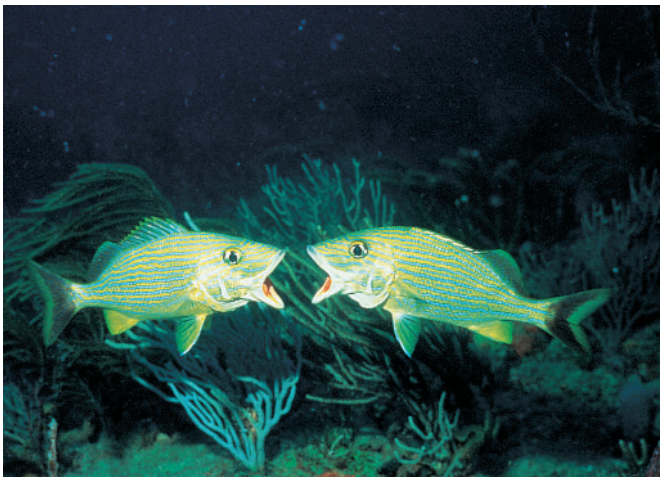
Migratory behavior of marine and freshwater fishes may be controlled by annual, seasonal, lunar, or daily cycles that trigger movement from one location or depth to another. Pelagic fishes, such as marlins (Istiophoridae) or dolphinfishes (Coryphaenidae), migrate great distances annually. These species, and numerous others, track changes in water temperature and move from winter to summer grounds, or vice versa, for feeding and reproduction. Many river species, especially in larger rivers prone to flooding, migrate annually or seasonally to take advantage of the new spawning habitats and food sources made available when bottomlands are flooded. Fishes may migrate from one body of water to another for reproduction, and their progeny often migrate back from where their parents came. Diadromous, catadromous, and amphidromous migrations and subsequent recruitment of young may be triggered by annual or seasonal stimuli. Vertical migrations allow fishes to track the movements of potential prey as they migrate up and down in the water column.

Atlantic manta ray (*Manta birostris*) with cleaner fish in the Gulf of Mexico. (Photo by Animals Animals ©Joyce & Frank Burek. Reproduced by permission.)

Communication

Communication is an important component of fish behavior. The transmission and reception of information by a number of means facilitates social interaction, the partitioning of space, cooperative feeding, predation avoidance, and reproduction. Visual communication is important in all but the darkest or most turbid environments. Many freshwater and marine species possess color patterns that are helpful for species recognition, sex recognition, age determination, and for assessments of agonistic and reproductive states. Both black and white coloration and bright colors are utilized. Coral reef fishes, for example, are famous for their bright color patterns, or poster coloration. (Poster coloration, a term coined by Nobel laureate Konrad Lorenz, refers to the conspicuousness and potential advertising or function of bright color patterns in coral reef fishes. Such coloration is useful in intra- and interspecific communication during territorial interactions, aggregation formation and maintenance, or mating, and facilitates species recognition.) Color patterns may be permanent or temporary. The latter is under hormonal control in relation to the expression of certain behaviors. For example, some groupers assume temporary color patterns during social interactions. The detection of bioluminescent signals at night or in low-light habitats is another component of vision-based communication. Numerous deep-sea and deep-slope fishes utilize light flashes to communicate with conspecifics. Fishes also employ body and fin displays to communicate intentions during territorial encounters, courtship, and predation avoidance.

Several species of fishes communicate with sound. Sound production is used to warn predators, warn of predators, attract mates, attract conspecifics in school formation and maintenance, and to communicate intentions during agonistic, reproductive, and parental care interactions. Sound production also places fishes at risk from predation, as some predators have learned to locate sound producers and prey upon them.



Blue striped grunts (*Haemulon sciurus*) fighting. (Photo by Michael Patrick O'Neill/Photo Researchers, Inc. Reproduced by permission.)

Fishes produce chemical secretions known as pheromones, which may be detected by taste or smell. Chemoreception is significant for the recognition of conspecifics in catfishes (Ictaluridae), minnows (Cyprinidae), and other species. This recognition is important in establishing and maintaining social relationships, such as dominance hierarchies or territorial interactions. Parents and young in species that practice parental care of fry and juveniles, such as the cichlids (Cichlidae), employ chemical reception to identify each other.

Fishes make use of touch when communicating intentions during aggressive behavior, courtship behavior, and parental care. Electric communication in gymnotids, mormyrids, and some catfishes (Mochokidae and Ictaluridae) is also used for aggressive and courtship behaviors, and is especially helpful in waters where visual detection is greatly reduced or nonexistent. Electrical discharges made by these fishes are species specific. Variations in production properties, such as pulse length, interpulse length, frequency, and amplitude, allow these fishes to communicate or assess information about species identity, individual identity, sex, size, reproductive readiness, and level of agonistic behavior. The fishes also obtain information on the location of and distance between communicators in this way.

Behavior and habitat use

How fishes select and make use of habitat is determined by their behavior. In marine systems, especially coral and rocky reefs, pelagic larvae actively swim shoreward as they prepare to settle into a habitat. Prior to and during settlement they assess the suitability of that habitat. For example, damselfish (Pomacentridae) larvae settling onto a portion of a reef have been observed to reject this habitat, swim back up into the water column, and search for more suitable one. Post-larvae, juveniles, and adults all utilize a variety of patterns that allow them to compete or coexist with others already using a habitat. Agonistic behavioral displays are common. Sometimes, the behaviors involved are cryptic, in that fishes "sneak" into the habitat and become established without drawing attention to themselves. Size-structured schooling species likely join the school as larvae and exploit a repertoire of innate patterns that allow them to function cohesively with conspecifics. In shoals or mixed-species schools, members use a similar repertoire to join, maintain, or leave the aggregation. Solitary pelagic species employ a repertoire of behavioral patterns that allows them to swim, feed, and avoid predation in a habitat that provides little or no cover. If cover is present in the form of drifting pelagic algae, logs, or other flotsam or jetsam, small pelagic species seek shelter there. Some species, such as the sargassumfishes (Antennariidae), are adapted to life in floating sargassum, where they shelter from predators, ambush prey, and mate. Other fishes, such as juvenile butterfishes (Stromateidae), shelter within the tentacles of pelagic jellyfishes. Many small pelagic fishes recruit to floating structures, and larger predators are attracted in turn.

Benthic freshwater and marine species often adapt to specific conditions and make use of seemingly novel structures that provide shelter, feeding sites, or places for reproduction. In moderate or fast-moving streams, trouts and charrs learn to make use of rocks, logs, holes, undercut banks, and other forms of structure as shelter. Their swimming behaviors allow them to move up into the current, feed or chase off intruders, and return to their shelter sites. Sand-dwelling darters (*Ammocrypta*; Percidae) in slower moving streams rest on the sand, but bury into it to avoid predators. On coral reefs, various species use specific behaviors to burrow into sand, rubble, cobble, or mud in order to avoid predation, ambush prey, or rest. Fishes that employ burrows use those dug by other organisms or dig and maintain their own structures, often building multiple entrances or exits. They swim, hover, or rest near these burrows as they feed or engage in social interactions, but will dart quickly into an entrance if threatened. If resting inside a burrow, they may quickly escape via an alternate route if a predator is blocking or has entered one of the entrance points. These burrows are sometimes shared by more than one fish species or by invertebrates, such as snapping shrimps, in a symbiotic relationship. Other benthic fish use abandoned tubes made by polychaete worms or other invertebrates. These fishes swim out of these tubes to feed or mate, but return and move backward into them if threatened. Some tube-dwelling species use these structures as cryptic ambush sites from which they attack passing fishes. Shrublike corals, sea fans, and black corals all provide structures for a number of small reef species. These structures are shared because intra- and interspecific behavioral interactions define the use of space and reinforce order and structure within the coral head.

Social behavior

Agonistic behavior is employed by fishes to establish social dominance, defend territories, and ward off potential predators, and involves the use of displays given at increasing levels of intensity. The displays are fixed or modal action patterns, and the sequence of their use is often highly ritualized. The information communicated by a pattern or series of patterns in sequence is therefore recognized in the context of its use, and aggressive behavior leading to the injury of one or more parties in the interaction is often averted.

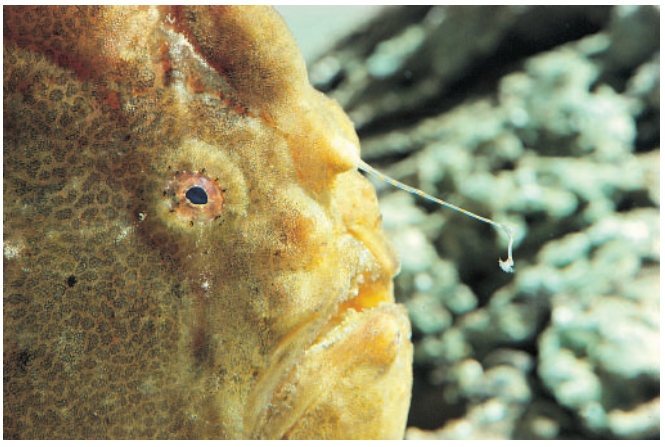
Dominance of one or more individuals by the agonistic behavior towards another of the same species occurs among groups of individuals, in shoals, and in schools. Dominance is expressed in either of two ways. First, a single individual may dominate all others who hold equal rank under the dominant fish. More commonly, a dominance hierarchy forms linearly, with a single alpha individual dominating others. The alpha is followed by a beta individual that dominates the remaining individuals, and so on. Dominance hierarchies such a this are often ordered on the basis of body size, with larger fishes dominating smaller fishes. They may also be ordered by different levels of aggressive behavior between individuals, with the more aggressive fishes dominating less aggressive fishes. Mating groups of sex-changing fishes also have hierarchies. For example, the mating group of the hawkfish *Cirrhitichthys falco* (Cirrhitidae) consists of a single dominant male, a large dominant female, and two or more subdominant females of variable size, which dominate one another on the basis of greater body size.

Agonistic behavior is used to defend living space, food resources, or mating groups and sites. This is known as territorial behavior. Territorial displays include the use of body displays, erect fins, color changes, sound production, chasing, or a combination of patterns. Defense may be against both intra- and interspecific intruders. The latter include competitors for food and space, but may also include potential predators of a defender's nest of eggs or free-swimming offspring. Territories usually consist of an area of relatively fixed size. The size of a territory varies within species and between species, usually as a function of size or sex, but will also vary in relation to the give and take of interactions with neighbors. A territory will often be nested in a much larger home range that is utilized by the fish or a group of fishes. Only that space that is actively defended by an individual is considered a territory. Territories may be permanent or temporary. For example, territories needed for courtship and spawning of a number of fishes are formed only during the breeding season or at certain times during the breeding season. Agonistic behavior increases during these times, but will often be absent during nonmating periods. Fishes may leave their home ranges or territories to form temporary multimale territories at courtship sites, known as leks, at which to attract females for mating. Some of these leks are "floating," in that their position may change relative to the location of females in the area. Territories required for feeding may be quite large, especially for larger predatory fishes, and may often greatly exceed the area defended for shelter space. Permanent territories often involve the defense of a shelter site. Males in single-male, multifemale, mating groups will defend their territories and those of the females contained within. Females, in turn, defend their smaller territories from intrusions by neighboring females within the same group. Mating sites of these fishes are defended in the same way. At the extreme end of territorial behavior is the defense of personal space, as seen in shoaling or schooling fishes that display to, or ward off, neighboring fishes who swim too close.

Territorial defense is also practiced by monogamous pairs of fishes. The best-known examples are the butterflyfishes (Chaetodontidae) on coral reefs. Pairs of butterflyfishes patrol a territory and may encounter potential competitors for food or space. These competitors include conspecifics (also usually in pairs), as well as other species that may utilize the same resources. Defense involves an exchange of ritualistic displays culminating in the departure of the combatants. Highly territorial butterflyfishes, not usually in pairs, chase intruding competitors away; however, noncompetitive species are usually ignored. Clustering behavior, in which one or more individuals within a group, or mosaic, of territories rises up into the water column to assess others in the mosaic without engaging in agonistic interactions, is an interesting offshoot of territorial behavior, and has been observed in damselfishes.

Salmon leap up a waterfall to return to the place where they hatched to spawn. (Photo by Randy Wells/Corbis. Reproduced by permission.)

Fishes form shoals or schools for protection from potential predators, foraging, overcoming the territorial defenses of individuals migration, and reproduction. Shoals are unorganized aggregations and may often be temporary in nature. They may consist of different species with a changing membership (heterospecific shoal), are relatively unstable, and may be dissolved and reformed quickly. Schools are organized or polarized aggregations that form permanently or temporarily. Generally, they are monospecific (contain only one species),



Tropical angler (*Antennarius* sp.) "fishing" for food using its elongated dorsal fin, wiggling its tip to simulate a small fish or worm. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

and membership is often age specific. Schools may dissolve at night for diurnal species, during daylight for nocturnally active species, or remain constant over a 24-hour period. Some schools dissolve under heavy attacks from predators, but reform afterward if sufficient numbers of fishes survive. The movements of schools are governed by a unique set of behaviors that determines position, synchronized movements, swimming speed, evasion, and flight.

Fishes have been found to be capable of transmitting traditional information socially. For example, certain benthic reef fishes follow predictable long-term routes between feeding and sheltering grounds as either darkness or dawn approaches. Experimental manipulations of the composition of a shoal of these fishes have shown that resident fishes can transfer information about the location of resting shelters to fishes new to the shoal during a dusk or dawn migration.

Fishes form symbiotic relationships with other fishes, or with invertebrates that share some common form of microhabitat, food, or need. An excellent example of shared microhabitat is seen in the anenomefishes (Pomacentridae) and the burrowing shrimp gobies (Gobiidae). Anenomefishes live in close association with anenomes, flowerlike benthic invertebrates related to corals that have poisonous nematocycts in their tentacles and are capable of inflicting an injurious or deadly sting. The function of these nematocysts is to deter predators and immobilize prey. Anenomefishes have developed defenses against the effects of the sting and make use of the tentacles for shelter and nest sites. Part of the anenomefish's defense is behavioral, in that its undulating movements within the tentacles communicate to the anemone that it is neither a threat nor some form of prey to be stung and ingested. In exchange, the anemonefish defends the anenome against potential predators, such as butterflyfishes, that feed upon the anemone's tentacles. Anenomefishes may also "groom" the anenome by removing foreign matter and feces, as well as consuming potential parasites. Shrimp gobies share burrows with one or more species of snapping shrimps of the family Alpheidae. The shrimp, which is usually blind, constructs a burrow that may be shared with one or two individuals of a given species. The goby, or pair of gobies, guards the burrow at its entrance while the shrimp maintains it. If danger approaches, the shrimp is alerted as the goby or gobies signal it with flicks of the caudal fin. If the threat continues, the goby or gobies will dive headfirst into the burrow and the shrimp will retreat. Often there is species specificity between shrimps and gobies, and there is some evidence that both the goby and the shrimp settle out of the plankton together as post-larvae, prior to the construction of their shared burrow. The behavior exhibited by the anenomefishes and anenomes, and the shrimp gobies and the burrowing shrimps, is known as a mutualistic symbiosis, in that parties benefit from the relationship. Other examples of mutualistic behavior relating to cleaning and the control of parasites, and commensalistic behavior, such as the relationship between remoras and large pelagic fishes, are discussed in the section on feeding behavior.

Reproductive behavior

Behavior is an essential component in the reproduction of fishes, and is essential for the identification of conspecifics, the attraction and selection of mates, the process of courtship and spawning, and, in a number of fishes, parental care. To perform these functions, fishes have developed a repertoire of behavioral patterns. These are often used in conjunction with some physical trait, such as a larger body size, elongated fin rays, larger hook-shaped lower jaws (kypes), well-developed humps on the forehead, and unique color patterns (temporary or permanent). These physical traits are coupled with one or more behavior patterns, whose use and intensity of use accentuate the traits. The products of sexual selection, these patterns and traits confer reproductive advantages to individuals in a given species population. Other patterns are essential for the physical act of spawning or breeding to occur, or for parental care to be successful.

Fishes identify conspecifics as potential mates by the recognition of species-specific morphological shape and form, color patterns, scents, or various behaviors. This recognition is not as easy as it seems because of variation in each as a function of sexual dimorphism or individual variation. Sometimes "mistakes" in species identification are made, and interspecific mating occurs. Most of these mating attempts likely fail, but occasionally functional offspring, or hybrids, result. Once species identity is recognized, the next step is to determine if the potential mate is of the opposite sex. Again, differences in morphology and color pattern or other factors accentuated by sexual dimorphism are recognized. If no such differences exist, then the use of behavioral patterns becomes an essential tool for the recognition of sex. Once sex is recognized, potential mates have to determine if they are attractive or suitable for one another and if they are ready to mate. Sexually selected traits and patterns are utilized to determine this. In many mating systems, females select mates. Females are attracted to males that appear stronger, fitter, and capable of providing the greatest investment for her offspring. Males utilize a series of behavioral patterns to convey this impression.

They may also emphasize the quality of their resources, such as feeding or sheltering territories, nest sites and qualities, or spawning site locations. Females assess these attributes and select the most attractive male or males, accordingly. Males, for their part, may wish to mate with the largest female or the most females possible. Larger females tend to be more fecund, thus increasing a male's opportunity to fertilize more eggs, pass down his genes, and achieve greater fitness. Mating with more than one female also increases fitness. Males compete with other males for access to females. The quality of their behavioral and physical traits and their use in intermale interactions, convey an advantage to one male over another.

Courtship patterns are used to attract mates, assess spawning readiness, and facilitate spawning or mating. A male employs a series of patterns to attract passing females or initiate courtship with females that form part of his mating group, and courtship bouts ensue with variable success. For example, in single male, multifemale mating groups (called "harems" by some authors), a male courts and spawns with each of his females in succession. Unfortunately for the male, this is not always easy. Individual variation in readiness to spawn among females means that a male may have to make repeated visits to females within his group before spawning takes place, and there is no guarantee that he will be successful in spawning with all females during a given spawning period. Sometimes the male is so busy attempting to spawn with one female that too much time passes and the "spawning opportunity window" closes before he can mate with others in his group. Alternatively, especially at dusk when light levels are falling, the male may become the target of a predator as he moves between females to court. Predator avoidance is costly because spawning opportunities may be lost. Worse, from the male's perspective, is that he might become lost, and control of the mating group will pass to a sex-changing female within his group or to another male from outside the group. Females are also at risk while waiting to court and spawn, and this threat may affect spawning readiness.

If courtship is successful and the male is able induce the female to spawn or mate, another series of patterns comes into play, which help the pair (or group, if spawning is in an aggregation) synchronize their activities so that the spawning or mating event is successful. Some of these patterns are as gentle as a male nuzzling the female's abdomen during a paired pelagic ascent, as in some of the marine angelfishes (Pomacanthidae). Other patterns, such as a sharp-toothed male shark grabbing a female's flank so that he can insert his clasper inside her and attempt internal fertilization of her eggs, are more forceful.

Modes of reproduction classify how fishes reproduce physically. The mode itself is not specific to a single taxonomic group, but may be shared by many taxa regardless of their phylogenetic affiliation. Criteria are defined based upon the degree of parental care, if any, invested. Thus, fishes may fall into three general guild categories: those that do not guard offspring, those that guard offspring, or those that bear offspring. Nonguarding species spawn openly upon substrates, either pelagically or benthically, or they hide their broods. Open pelagic spawning occurs in the water column. Fishes swimming in the water column engage in courtship and release eggs. Benthic fishes swim upward into the water column and release eggs and sperm at the apex of the spawning rise or rush. Spawning may be paired or in groups. Open benthic spawning includes the release of eggs onto the substrate (rocks, cobble, etc.), with the resultant larvae being either pelagic or benthic. Benthic spawning may also occur on plants as an obligatory or nonobligatory function, or on sand. Brood hiders deposit their eggs on the bottom, in caves, on or in invertebrates (such as corals, bivalve mollusks, and crinoids), or on beaches during a tidal cycle. They may also deposit eggs on a substrate that is prone to annual desiccation, in which case the eggs are adapted to resist this and hatch out when wet conditions return.

Spawning aggregations are a specialized behavior, and are formed by migrations of fishes to specific sites for courtship and spawning. There are two general types of spawning aggregations: resident and transient. Resident aggregations occur locally, in that members of the aggregation are drawn from the general area in which the aggregation forms. These aggregations usually form on a daily, semilunar, or lunar frequency. Transient aggregations consist of fishes that are drawn from a much larger area and population. Some species of groupers, for instance, migrate hundreds of miles along coastal waters in the Gulf of Mexico and Caribbean, and the number of individuals forming the aggregations can be in the hundreds or even thousands. These aggregations usually form annually or seasonally in relation to the lunar period. Both kinds of aggregations form at sites that appear to facilitate mating and the dispersal of eggs and larvae.

Guarders include those fishes that choose the substrate they spawn upon with subsequent guarding of the offspring. The substrates chosen include rocks, plants, terrestrial structures (such as overhanging leaves or flooded grasses), or the water column. Nest spawners construct simple or complex nests to attract females, deposit eggs, and provide parental care. Nests are made from a variety of materials, including gravel and rock, sand, holes, plant materials (with or without a "glue" secreted by the male), anenomes, or bubbles. In the latter case, males of some species make the nest by blowing bubbles of air and mucous onto an object or even the underside of the surface of the water. Miscellaneous materials are also utilized in nest construction. Generally speaking, nest construction is more common in freshwater than in marine species.

Fishes that bear young are either external or internal bearers. External bearers include mouth brooders, pouch brooders, gill chamber brooders, forehead brooders, skin brooders, or brooders that transfer offspring between one individual and another. Fertilization may be external or internal depending upon the taxon. Internal bearers have internal fertilization. Oviparous fishes deposit egg cases on the substrate; these eggs hatch externally. Ovoviviparous fishes retain fertilized eggs until they hatch and then release offspring "live." Viviparous fishes retain fertilized eggs that, as embryos, develop internally and are also released live. There are two forms of this strategy. The first is yolk-sac viviparity, in which the egg's yolk sac is attached to the digestive system of the developing embryo. The second is placental viviparity, in which a placental

connection between the mother and the developing embryo occurs. Not all internally fertilizing fishes have internal bearing, however. For example, glandulocaudine characins (family Characidae) and many catfishes of the family Auchenipteridae have internal fertilization but are egg scatters. Similarly, members of the genus *Campellolebias* (family Rivulidae) have internal fertilization but are egg hiders.

One specialized form of live bearing is parthenogenesis, in which young are produced by a female without the fertilization of eggs by males. There are two forms, gynogenesis and hybridogenesis. In gynogenesis, an egg is activated following mating with a male of another species, but no fertilization of that egg occurs. The egg develops within its mother and is born as a female identical to the mother. In hybridogenesis, mating with a male of another species also occurs, but the egg is fertilized. The male's genetic component is discarded and the egg develops into a female identical to the mother.

Fishes select sites for reproduction in a variety of ways. For instance, salmons, trouts, and charrs make short or long-distance migrations to spawning habitat. Spawning occurs in gravel beds or other suitable substrates and includes the preparation of a redd, a depression made into the substrate where eggs are deposited, fertilized, and buried. In other fishes, nest sites may be placed within the territory of a male (or less commonly, a female) and are defended after spawning takes place between the nest owner and one or more mates. Nest sites may also be located within a home range of a temporary or permanent pair of fishes. There the eggs are deposited and fertilized, after which the site is abandoned. In some species, there is no nest at all, and eggs are merely broadcast over a suitable substrate. Spawning sites of pelagic species follow similar rules. Sites may be within a territory or cluster of territories, and are defended against intruders (usually same-sex rivals). Sites may also be used on a regular basis, due to some physical feature that may favor pelagic spawning, but are not defended.

Parental care of eggs and offspring is most often practiced by males than females, and is more commonly seen in freshwater rather than marine species. In some species of African cichlids, such as members of the genus *Lamprologus*, care is provided by helpers that are usually related to the parents and offspring. These helpers forego the opportunity to breed at this time, but manage to realize some sort of evolutionary fitness by learning parenting behaviors and by protecting offspring that carry a fraction of their own genes.

Care behaviors provide defense and maintenance of offspring. Parents protect the eggs and larvae in their mouths, brood pouches, or other structures, but also attack intruders that attempt to prey upon them. Defense also includes herding or shielding larvae or post-larvae from attacks. Maintenance behaviors include blowing on eggs to provide them with oxygen and to remove detritus or other undesirable objects (including dead eggs). Parents also provide alternative food sources for growing larvae. For example, some cichlids secrete a skin mucous that provides nutrition for their young, who ingest this by "glancing off" the flanks of their parents where the mucous is deposited. Intertidal species may wrap their bodies around an egg mass to shield it from desiccation during low tide. A freshwater tetra, *Copella* sp. (Lebiasinidae) from South America, lays its eggs on the leaves of overhanging terrestrial plants to avoid predation, and splashes water on the egg mass to provide it with oxygen and to prevent desiccation. Electric eels and some bagrid catfishes produce infertile trophic eggs to feed their free-swimming young.

A number of fishes practice alternative mating tactics that exploit certain behaviors to a strategic advantage. For example, in mating systems with paired spawning, the pair consists of a dominant or parental male and a female. Other, smaller, males in the vicinity, known as satellite males, mimic females both in color and behavior. The satellite males approach a mating pair and, if successful at "fooling" the male, will not be chased off. Then the intruder inserts itself into the dominant male-female courtship bout and attempts to fertilize at least some of the female's eggs. In other cases, smaller "sneaker" males use stealth to approach a mating pair, then quickly streak or dart into the pair's spawning bout as eggs are released to fertilize a portion of them. Among nesting fishes, both tactics have been observed in the bluegill sunfish (*Lepomis macrochirus*; Centrarchidae), whereas the latter has been seen in salmons.

In pelagic spawning fishes, smaller satellite males will streak into the water column to join a pair during their spawning ascent and fertilize part of the female's eggs. This has been observed in a number of groups, and variations on the theme occur. Two independent teams of researchers studying the reproductive behavior of the "haremic" Japanese sandperch (*Parapercis snyderi*; Pinguipedidae), observed repeated sneaking behavior by dominant males from neighboring mating groups instead of by satellite males. One team found that these males sneak fertilizations in neighboring groups after spawning with all the females in their own groups had been completed for the night. The other research group also observed this pattern, but found that dominant males temporarily abandoned courtship with their own females and carried out "sneak" fertilizations in a neighboring group in close proximity to their own location, when the opportunity presented itself. Males also spent considerable amounts of time and effort defending their groups from sneaking neighbors. The downside of these behaviors was that the opportunity to mate with their own females was lost and the females mated with other males while their males were busy.

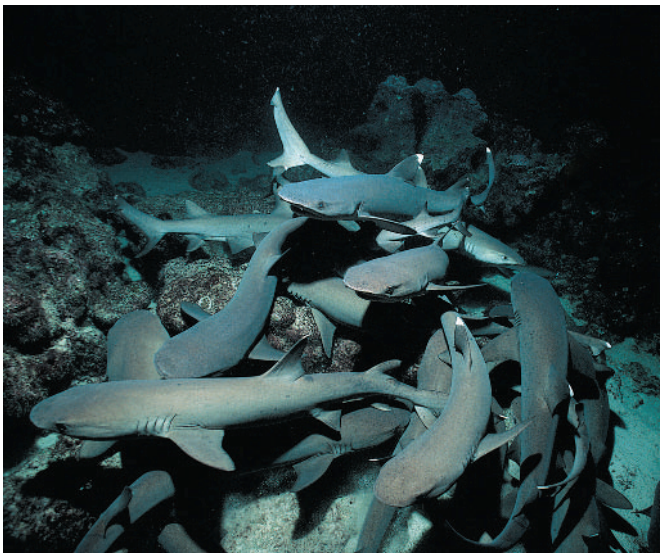
Lizardfishes (*Synodus dermatogenys*; Synodontidae) have two strategies that depend upon local population size and sex ratio. If the population is relatively low, and the numbers of female and males are approximately equal, paired courtship and spawning occurs. If, however, the population size is larger and males outnumber females, then a different strategy prevails. In this case, males form floating leks at sunset to display to larger females as the latter move about the spawning site. One male may be more successful and joins the female as she rises into the water column to release her eggs. As the female and male ascend, however, they are joined by other males, who all contribute sperm toward the fertilization of the eggs. Females do appear to exercise control over the timing of the spawning and the composition of the group. Unlike females of many other pelagic spawning reef species, female

lizardfishes may spawn more than once during an evening. As courtship continues, the female rises to spawn again and is joined by more than one male. If, however, only one male joins her, she will abort the spawning ascent, return to the bottom, and wait for courtship from the group of males to resume. Females seem to pursue this strategy of group spawning in order to assure complete fertilization of their egg masses. The male closest to her in an ascent, the one she chooses from the others as the most attractive, will likely fertilize a significant proportion of her eggs, but the contributions of the other males may promote both genetic diversity and completion of the job!

Feeding behavior

Fishes use a variety of behaviors while feeding to detect and capture prey, extract plant materials, or to sift sediments to extract objects of nutritional value. Planktivory by fishes occurs during the day and at night. During daylight, hovering planktivores such as fairy basslets (Serranidae: Anthiinae), some freshwater sunfishes, damselfishes, angelfishes, certain triggerfishes (Balistidae), and many other species, feed upon zooplankton or phytoplankton by plucking individual plankton out of the water column. Plucking is accomplished with specialized mouthparts or by rapid movements of the mouth. The mola (Molidae), and other species that feed upon macroplankton or mesoplankton in the water column, forage in a similar fashion. Garden eels (Congridae) and other burrow-dwelling planktivores emerge partially from their burrows to feed upon plankton that drift past in the current. Schools of fusiliers (Caesionidae) dart erratically in the water column as they grab and feed upon plankton they detect there. Alternately, fishes such as whale sharks (Rhyncodontidae), basking sharks (Cetorhinidae), manta rays (Mobulidae), herrings, anchovies (Engraulidae), scads (*Decapterus* spp.; Carangidae), and similar species open their large mouths and strain the plankton from the water column as they swim. Fishes with smaller mouths, such as reef herrings and flyingfishes (Exocoetidae), also strain plankton in the water column. At night, a new set of planktivores emerges from shelter to feed upon pelagic and demersal plankton in the water column. These include squirrelfishes and soldierfishes (Holocentridae), cardinalfishes (Apogonidae), bigeyes (Priacanthidae), along with a host of deep-dwelling species. These fishes use their large eyes and other well-developed senses to detect and feed upon plankton.

Herbivory in marine fishes is more pronounced in tropical than in temperate species. Among the tropical fishes, halfbeaks (Hemirhamphidae), sea chubs (Kyphosidae), damselfishes, parrotfishes (Scaridae), blennies (Blenniidae), rabbitfishes (Siganidae), and surgeonfishes (Acanthuridae), are the prominent groups. In freshwater systems, numerous species feed upon benthic algae, emergent plants, and even seeds and fruits from terrestrial plants. Some marine groups, such as the butterflyfishes, angelfishes, filefishes (Monacanthidae), and triggerfishes, include species that are omnivorous and feed upon benthic algae. In temperate marine waters, some members of the Sparidae (porgies), Kyphosidae, Aplodactylidae (sea carps), Odacidae (rock or weed whitings), and



Pack of whitetip reef sharks (*Triaenodon obesus*) hunting at night in the Pacific Ocean, near Cocos Island off Costa Rica. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

Stichaeidae (pricklebacks) are more dependent upon plant life. Freshwater omnivorous species, such as the carp and its relatives (Cyprinidae), and a number of characins (Characidae), often include plant materials as a significant part of their diet.

Herbivores feed by grazing or browsing, and are capable of learning what species of plant are edible and what are toxic. Access to edible benthic algae, sea grasses, or other plant materials may be as simple as swimming into a given area and stopping to graze or browse. Parrotfishes feed on zooxanthellic algae contained in coral skeletons by using their specialized beaks scrape algae off rocks or dead corals. They also bite off chunks of the coralline skeleton as they graze. The parrotfish's pharyngeal teeth crush the chunk within the mouth cavity, swallow and extract the algae, expel the resulting coralline sand. Territorial species, such as certain damselfishes known as "farmer" fishes, actively maintain patches of desirable species of algae that they tend, defend, and feed upon. Other herbivores attempting to feed upon this patch (or patches of algae not tended, but within the territory of any herbivorous species) are turned away. Fishes defending the patches must be overwhelmed before other herbivores can gain access to this resource. One way to accomplish this is for the grazing or browsing species to form schools that can move into a territory and easily outnumber the defender. One form of this type of school, the heterospecific or mixed-species shoal or school, consists of fishes of a number of species (including nonherbivorous fishes) that move about the bottom. Membership in the school is temporary, and its members not only gain protection from schooling but, more importantly, are able to breech the defenses of a territorial herbivore to feed upon the algae it attempts to protect.

Feeding by herbivorous monospecific schools takes place both at night and during the day. For example, unicornfishes (Acanthuridae) form schools that graze on sea grass flats at

night. Their efficiency at feeding upon sea grass and benthic algae there is analogous to a giving the flat a good haircut.

Predators rely heavily upon one or more sensory systems in their search for prey. Among benthic species, ambush predators such as scorpionfishes (Scorpaenidae), flatheads (Platycephalidae), and sculpins (Cottidae) use vision to detect passing prey. Scorpionfishes and many sculpins remain motionless until they detect prey and estimate the distance to it. The predator then engulfs the prey by rapidly opening its mouth and sucking it in. Flatheads grab the prey with a mouthful of teeth, and manipulate and swallow it. Other ambush predators, such as lizardfishes or hawkfishes, launch themselves into the water column or down to the substrate to grab prey. Freshwater pikes and pickerels (Esocidae), groupers, basses (Centrarchidae), the Murray cod (Percicthyidae), and the barramundi (Centropomidae) utilize structures, such as submerged trees and stumps or weed beds, to mask their presence as they ambush passing prey. Their acute vision allows various trout species in streams to identify and assess aquatic insects carried by surface and subsurface currents. At night, the enlarged eyes of many nocturnal predators allow them to detect, track, and attack prey on the bottom or in the water column.

Other sensory systems, such as taste, touch, and chemoreception, allow fishes that prey on benthic invertebrates and smaller fishes, such as catfishes (various families), goatfishes, threadfins (Polynemidae), freshwater eels (Anguillidae), and moray eels (Muraenidae), to detect prey buried just beneath the surface of the substrate. Similarly, electrical receptors known as ampullae of Lorenzini allow elasmobranches, such as sharks and rays, to detect minute electrical currents generated by prey buried beneath sand, rubble, or mud; locate their position; and feed upon them. Knifefishes (Gymnotiformes) of South America and the Mormyridae of Africa use other organs to generate weak electric fields that allow them to detect prey in murky water.

In the pelagic realm, vision, olfaction, touch, and sound detection are important sensory components of predatory behavior. Swiftly moving predators, such as tunas (Scombridae) and billfishes (Istiophoridae), rely upon keen eyesight to track and hunt their swiftly moving prey. Predators, especially sharks, also rely upon the smell of prey, and in particular, the smell given off by injured prey, to detect them. Low frequency sounds generated by the movement of prey, whether swimming or struggling, are detected by the predator's lateral line system. These vibrations are felt, rather than heard, by the lateral line receptors. Higher frequency sounds generated by prey are detected by the inner ear and direct it to the location of the prey.

In deepwater environments, visual capabilities may be reduced in favor of other senses in some species, but accentuated in others. Deepwater predators with large eyes can detect bioluminescent flashes generated by potential prey. Chemoreception, hearing, and lateral line senses are also important in prey detection in waters where darkness prevails and little or no light penetrates from above.

The pursuit of prey varies among predatory species. Ambush predators frequently employ camouflage and position themselves among rocks, corals, or marine plants to conceal themselves until they can detect and ambush prey. Some ambush predators use lures fashioned from modified fin rays or other body parts. These lures, which may resemble a small fish or invertebrate in shape, are waved about to attract the prey. This behavior, sometimes referred to as aggressive mimicry, occurs in a few shallow and deepwater predatory families of fishes. In deepwater species, the lure may be bioluminescent. Other predators, such as juvenile snappers (Lutjanidae) or hamlets (Serranidae), mimic nonthreatening species such as damselfishes to get closer to prey. Predators, such as trevallys (Carangidae), often rapidly patrol the bottom throughout the day and night in search of prey that cannot retreat to shelter quickly enough to escape being eaten. These predators may also attack schooling baitfish species in the water column singly, in pairs, groups, or schools. Barracudas (Sphyraenidae) rest motionless in the water column, then strike rapidly, sometimes over a distance of several meters, at an unwary fish in the water column or on the bottom. Schools of salmon, striped basses (Moronidae), amberjacks (Carangidae), bluefishes (Pomatomidae), and tuna (Scombridae) rapidly chase and slash schools of fleeing baitfishes, and may also herd them while attacking. Other species, such as some barracudas and lionfishes (Scorpaenidae), hunt in packs and often utilize structures, including reef and cave walls and even suspended fishnets, to act as barriers to aid in escape. At sunset, a pack of lionfishes assembles and gathers near a school of sweepers (Pempheridae) that is emerging for the night. Then the lionfishes extend their large pectoral fins and use them to push the sweepers into an increasingly small aggregation that is ultimately trapped between the pack of lionfishes and the reef wall. The predators then rapidly inhale the sweepers with their large mouths as they try to escape. Other predators, such as groupers and large soapfishes (Serranidae), take advantage of this behavior to ambush escaping sweepers.

Many species detect prey hidden in bottom sediments and then dig or sift them out. A number of these predators have specialized teeth, mouths, or gills that allow them to do this; others fan the sediments to expose the prey. Some fishes, such as certain wrasses (Labridae) and trevallys, allow other fishes, such as stingrays and goatfishes, to do the digging for them. These predators follow the bottom-foraging species and feed opportunistically upon whatever may be exposed. Barracudas have been observed hanging motionless in the water column above nests of large triggerfishes (*Pseudobalistes* spp.). The triggerfishes constantly tend these nests by rearranging the substrate and turning over rocks, and in doing so they expose or startle prey fishes or other organisms. When this happens, the barracudas quickly rush down to the exposed prey and grab it before the triggerfish can respond.

Pelagic deepwater species ascend the water column as night falls and may rise hundreds of meters toward the surface as they track their prey. Some species are following the similar movements of pelagic invertebrates upon which they feed. Others track these fishes as prey, and some species, such as the snake mackerels or oilfishes (Gempylidae), have feeding behaviors that appear to be similar to shallow water species, such as barracudas (Sphyraenidae) or wahoos (Scombridae).

A number of predators employ mechanisms or behaviors that allow them to stun or otherwise immobilize their prey before they eat it. For example, torpedo rays (Torpedinidae), electric eels (Electrophoridae), electric catfishes (Malapteruridae), and some stargazers (Uranoscopidae) discharge a strong electrical current that stuns passing prey. Some wrasses (Labridae) smash their invertebrate prey with or against rocks. Archerfishes (Toxotidae) stun and knock down insect prey resting on mangrove branches or emergent grasses above the water surface by shooting a stream of water "bullets" at them. Billfishes and the swordfish (Xiphiidae) utilize their bills to herd, stun, spear, or slash their prey before eating them. Hammerhead sharks use their unique cephalic lobes to pin down stingrays, a favored prey. Sharks and barracudas use sharp teeth to capture and cut prey into smaller pieces before they are eaten. Sharks also take bites out of larger prey, such as whales, without capturing them. Relatively diminutive fishes, such as the poison-fang and fang blennies also practice this behavior. These small predators hover in the water column and launch themselves at passing fishes to bite off a scale or small piece of flesh. Fishes in the genus *Aspidontus* mimic bluestreak cleaner wrasses (*Labroides dimidiatus*), approaching fishes that may be fooled into thinking they will be cleaned, but end up being bitten. Juveniles of larger predators, such as the leatherback, *Scomberoides lysan* (Carangidae), also engage in this behavior. Scale-eating or biting off small pieces of flesh is also practiced in tropical freshwater fishes of Africa and South America. Specialized genera of scale-eating African cichlids (Cichlidae) include *Perrido*dus and *Plecodus* from Lake Tanganyika, and *Corematodus* and *Genyochromis* from Lake Malawi. Fin-eating is practiced by characoid fishes of the families Citharinidae (genera *Ichthyoborus*, *Mesoborus*, and *Phago* from Africa) and Characidae (subfamily Serrasalminae, the piranhas and their relatives; genera *Catoprion* and *Serrasalmus* from South America).

Cleanerfishes, including the cleaner wrasses *Labroides* and *Labropsis* (Labridae), cleaner gobies (*Gobiosoma*), and some butterflyfishes establish cleaning stations along coral or rocky reefs, where they attract and clean the "client" fishes that approach. The cleaners swim in a regular pattern of movements. The client fishes, responding to the swimming behavior and distinctive color pattern of the cleaner, as well as to the location of the cleaning station, assume a posing posture to signal that cleaning is required and may begin. The cleaners then forage along the client's body, feeding on parasitic copepods and other parasitic organisms, along with any damaged tissues. Cleaner wrasses and gobies also enter the mouths and gill cavities of their clients, including large predators like groupers and moray eels, without being preyed upon. This type of behavior is a mutualistic symbiosis, because both the cleaner and the client benefit. Cleaning behavior has also been observed in freshwater fishes, including some members of the family Cichlidae. A pelagic variation of this behavior is practiced by remoras or sharksuckers (Echeneidae). These fishes attach themselves to large predators, such as sharks, billfishes, turtles, and whales, and hitchhike as their hosts swim. In turn, the remoras feed upon parasitic copepods on the host, but will also take advantage of scraps left over from the host's feeding bouts. This behavior is a commensalistic symbiosis, in that the cleaner gains while the client neither benefits or loses out.

Parasitism by marine fishes is not a common strategy, but it does occur in a number of different species. Internal parasites include the pearlfishes (Carapidae) that live in the gut cavities of seacumbers and large starfishes, where they feed upon gut tissue. The eel-like *Simonchelys parasitica* (Synaphobranchidae) has been found burrowed into the flesh of various bottom-dwelling fishes, but has also been recorded from the heart of a mako shark, a fast-swimming pelagic species. In freshwater fishes, however, catfishes of the tropical Amazon family Trichomycteridae are parasitic. Most species attack gill tissues of larger fishes, but members of the genus *Vandellia* are known to parasitize the urethra of mammals, including humans, causing considerable harm. Lampreys (Petromyzontidae) are external parasites, which attach themselves to the skin of their prey and feed upon tissue and body fluids with their specialized mouths.

Fishes that feed upon detritus use their mouths to scoop up sediments, from which they extract detrital materials with their pharyngeal teeth and expel sediments through their gills. Scavengers feed upon dead and dying fishes or other organisms and play an ecological role. Fishes bite or peck at the body of the organism to remove chunks of flesh. Some fishes, such as the deepwater hagfishes (Myxinidae), are specialized to enter the body cavity of dead fishes to feed upon them internally.

Predator avoidance behavior

Marine fishes have evolved a number of mechanisms and behavioral strategies to avoid predation. These include color patterns and modifications of body structure to provide camouflage, mimicry, or warnings of toxicity. Color patterns that disrupt the fish's outline, reduce its contrast against background coloration, or allow it to blend into the background all provide camouflage and protection from predation. These same attributes also favor predators who wish to hide from their prey. Countershading (dark color dorsally and pale or white ventrally) and reverse countershading (pale or white dorsally and dark ventrally) obscure the fish when it is viewed from above or beneath. A silvery or mirrorlike coloration, as seen in herrings, tarpons (Megalopidae), ladyfishes (Elopidae), smelts (Osmeridae), carps and minnows, and mullets (Mugilidae), reflects light and confuses potential predators. Fishes that are relatively transparent, such as in the glassfishes (Channidae) and some cardinalfishes, are difficult to see, especially in low light conditions. Similarly, modifications to the skin, fin rays, or other portions of the body can convey similar benefits. For example, the sargassumfish (Antennariidae) has modifications, which, in conjunction with its greenish brown coloration and hovering behavior, allow it to resemble sargassum algae. Pipefishes and seahorses (Syngnathidae), and some filefishes, have similar adaptations. Adult leaffishes (Nandidae) and juveniles of a number of species, including spadefishes and batfishes (Ephippidae), combine a color pattern with behavior to resemble inedible objects such as leaves.

Warning coloration informs potential predators that a fish is (or is giving the impression of) being toxic and should be ignored. The juveniles of some species of sweetlips (Haemulidae) have color patterns and behaviors that allow them to

mimic toxic nudibranches and flatworms. Other fishes with toxins in their skin or organs, such as various tobys or sharpnose puffers (*Canthigaster* spp.; Tetraodontidae), have color patterns that advertise their toxicity. One species of filefish, *Paraluteres prionurus*, is nonpoisonous, yet is afforded protection from predation because it has a color pattern and behavior that exactly mimics the black saddled toby (*Canthigaster valentini*), and, to a lesser extent, the crowned toby (*C. coronata*).

Behavioral responses to perceived threats detected by senses such as vision, hearing, the lateral line, and smell may be rapid or subdued. These responses are used by solitary individuals but are accentuated in aggregations or schools. Many species react swiftly to the sight of an approaching predator or to the detection of noises or pressure waves generated by its approach. Flight avoidance, usually in the form of rapid or erratic swimming away from the predator, occurs in the water column. Some species, such as flyingfishes, halfbeaks, and needlefishes (Belonidae), leap above the surface of the water and may coast for a few to several meters in the air before entering it again. As a school or aggregation, reef herrings and other baitfishes leap repeatedly into the air as they flee approaching predators. Schooling behavior provides significant predation avoidance benefits because of the fact that there is safety in numbers. Most predators have to target a single individual to successfully prey upon it. The presence of many individuals within a school means that, with more prey to choose from, the chances of any one healthy individual of being preyed upon is reduced as the school takes flight.

Fishes with less energetic responses than the reef herrings, such as lionfishes and other scorpionfishes, merely erect pectoral and dorsal fins that have poison-tipped spines to detract predators. Other fishes with poisonous spines show a similar behavior. Adult pufferfishes (Tetraodontidae) and porcupinefishes (Diodontidae) inhale water and inflate their bodies to avoid predation by all but the largest predators. These fishes may also be poisonous or have spines that make ingesting them difficult. Other species, such as garden eels (Congridae), sanddivers (Trichonotidae), tube blennies, burrowing gobies, and triggerfishes duck into holes or burrows. Triggerfishes can "lock themselves in" their holes by extending their dorsal and anal fin spines. Similarly, soles (Soleidae), flounders (Bothidae), and their relatives bury themselves in the sand. At night, sleeping parrotfishes wedge themselves into the reef and secrete a somewhat gelatinous cocoon that allows it to detect predators by touch if the cocoon is violated.

Another behavior normally attributed to birds but also observed in some species of reef and freshwater fishes is mobbing. Mobbing serves to ward off an intruding predator by displaying to or attacking it in number, but also to warn conspecifics of the intruder. For example, the damselfish *Pomacentrus albifasciatus* maintains territories adjacent to conspecifics on reef flats. If a predator, such as a moray eel or scorpionfish, enters the area, those damselfishes closest to the intruder rise into the water column and display their erect fins as they dance in front of, behind, or along the flank of the intruder. These damselfishes are soon joined by others from the territorial matrix, and together they mob the intruder until it leaves the area. This damselfish also appears to be able to recognize which kind of danger the intruder may pose before mobbing it. If the intruder is a scorpionfish, the damselfishes avoid displaying near its head and focus their attacks along the posterior flank or tail, presumably because scorpionfishes have large mouths and are capable of extremely rapid feeding attacks. However, if the intruder is a moray eel, the damselfishes also mob in the region of its mouth because it is relatively smaller and the eel's feeding behavior is different.

Behavior, evolution, and conservation

The behavior patterns in fishes evolved over countless generations, largely in response to pressures from natural and sexual selection. These behavior patterns are distinct and measurable, and they are just as much characteristics or traits as those based upon morphology or biochemistry. Although general patterns among different, and often quite divergent, species exist, the applications of these patterns and their subtle differences are often unique. Similarity in patterns may be a function of convergent evolution, common descent among related groups, or an affinity among species. Differences in patterns may be the result of a lack of affinity or may be subtle changes in application within a group of closely related species. The study of phylogenetic relationships among species by the comparative method provides an understanding of the patterns of behavior observed, as well as the processes that underscore their evolution within species. This field of study, known as historical ecology, has great utility in ascertaining patterns of character development between and within species, and has predictive power in instances where information on a particular species within a group of related species is relatively lacking. This method also allows for testing hypotheses that may confirm the validity of the prediction.

The methods of historical ecology in the study of fish behavior have considerable utility as tools for predicting how fishes behave under exploitation, habitat destruction, or other problems addressed in the science of conservation biology. Conservation efforts, especially in highly diverse systems, are often stymied because of a lack of information on the biology and behavior of some fishes within those systems. As detailed studies of most groups are lacking, some considerable effort has been expended upon understanding the biology and behavior of a relatively few species within these systems. Generalizations are feasible for attempting to understand species that are less well studied. However, only the steady collection of data coupled with the predictive advantages of historical ecology allows scientists to understand the larger picture so they can convey to fishery managers the information necessary for the design and implementation of effective conservation and management plans.

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Terry J. Donaldson, PhD

Fishes and humans

Overview

Fishes have figured prominently in human lives, cultures, and economies since ancient times. Fish themes appear in diverse aspects of human culture, including mythology, religion, literature, and art. In addition, fishes are important to humans as a source of food and income; thus, the quest for fishes played a large role in historical patterns of exploration, settlement, and even war. Fishes are the central focus of recreational activities enjoyed by many as well. Despite their value to humans, fishes are often negatively affected by the direct and indirect consequences of human actions. As a result, many fish species are threatened or endangered, and some have become extinct in recent years.

Fishes in human culture

Mythology and religion

Throughout history, fishes appeared in the legends, myths, and folklore of a variety of cultures. In many societies, fishes were associated with deities, perhaps indicative of the value and mystery of fishes in ancient cultures. In Iran and Babylon, archeological evidence revealed a deity with human legs covered by the full body of a fish. In Syrian culture, the mythical goddess of generation and fertility, Atargatis, was represented as the body of a woman with a tail of a fish—a depiction that gave rise to the image of mermaids. The ancient Egyptian deities Isis and Hat-Mehit were associated with fishes; due to the abundance of fishes available during the spawning season in the Nile Valley, these goddesses symbolized fertility. Many other indigenous cultures recognized deities that were believed to protect fish stocks and those persons that harvested fishes.

In some myths, fishes interact with deities in other ways. For example, two fishes derived from Greek mythology are visible in the sky each night—those of the constellation Pisces. According to this myth, Aphrodite, the goddess of love and beauty, was walking along the Euphrates River with her son, Eros, when they encountered the monster Typhon. One story suggests that Aphrodite and Eros jumped into the river, where they were transformed into fishes and fled. In another version of this myth, two fishes carried the mother and son to safety. Both versions imply that fishes can confer protection to deities.

Fishes continue to serve as important symbols in modern Christianity. The Greek word for fish, *ichthys*, is derived as the acronym for the biblical phrase *Iesous Christos Theou Hyious Soter*, which translates to "Jesus Christ, Son of God, Savior." The activity of fishing plays a central role in a variety of encounters between Jesus and his disciples, as he instructs them to be "fishers of men." It is believed that the fish symbol formed by two half-crescents arose as a way for persecuted Christians to identify themselves to one another in ancient Rome; this symbol remains widely used by Christians today and has been adopted in modified forms by those advocating alternative beliefs to certain Biblical teachings.

Literature and art

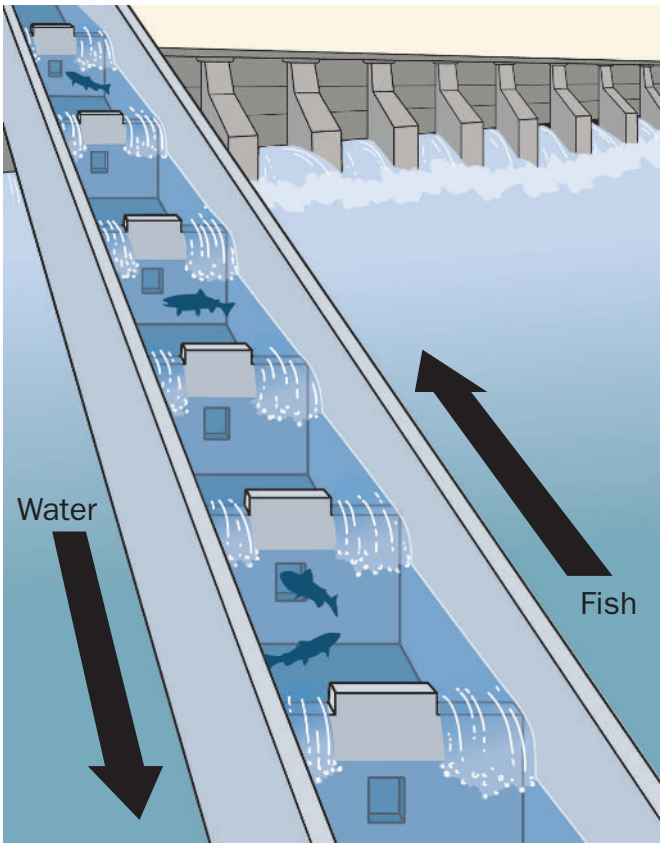
Many legends in classical and medieval literature convey tales of fishes as monstrous sea creatures that invoke fear into even the bravest humans. In his epic Roman poem *The Pharsalia*, Lucan suggests that large remoras, or shark suckers, could impede the progress of sailing and naval ships. Other stories tell of menacing sea serpents; some legends, such as that of the Loch Ness Monster, are perpetuated still today. In reality, many of the legendary "sea serpents" turned

From a small bowl with one fish to huge aquariums, people are facinated by the underwater world. This huge fish tank is at the Osaka Aquarium in Osaka, Japan. (Photo by Will & Deni McIntyre/Photo Researchers, Inc. Reproduced by permission.)

out to be nothing more than large eels, cuttlefish, squid, or sharks, and others were dismissed as figments of the imagination created by the interplay of light and water. Initially regarded as a folk legend, reports of "rains of fishes" date back to the third century A.D. Such incidents have been reliably documented in more recent years, and it is believed that violent storms may sweep fishes from water bodies and drop them back to land as air currents dissipate.

Fishes have been depicted in artwork throughout cultural history as well. Hieroglyphics of the ancient Egyptians show precise details of many fishes from the Nile River. Many of these carvings remain preserved on the walls of tombs, as fishes were believed to lead people to and sustain them in the afterlife. Native Americans of the Northwest carve fishes, specifically salmon, on totem poles, thereby conveying myths and spiritual connections of their societies to fishes. Fishes have long served as popular subjects in Asian art, particularly that of the Chinese, through which they are often displayed on pottery, screens, and paintings.

Fishes continue to appear in many forms in literature and media of modern culture. Novels such as Ernest Hemingway's *Old Man and the Sea* and nonfiction works such as Sebastian Junger's *Perfect Storm* recount the challenges and rewards of the pursuit of fishes, while childhood stories such as Dr. Suess's *One Fish*, *Two Fish*, *Red Fish*, *Blue Fish* are widely recognized and adored. In addition, movies periodically revitalize myths and fears of fishes. In the movie *The Little Mermaid*, the myths of mermaids, serpents, and sea gods again come to life. In contrast, *Jaws* preys upon general unfamiliarity with shark behavior to instill viewers with fear of these dominant ocean predators.



Fish ladders provide passageway around dams for migratory adults headed up-river for breeding, such as salmon. (Illustration by Amanda Humphrey)

Human uses of fish

Historical fisheries

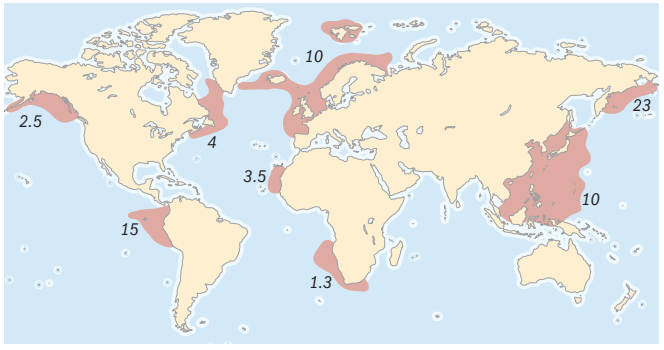
Fishes have been utilized by humans throughout history for food, income, and other purposes. Archeological records indicate that Egyptians exploited fishes in the Nile River from prehistoric times. Carvings record the types of fishes caught, fishing techniques, preparation methods, and the trade of fishes. The Egyptians used spears, hooks, weirs, and nets to capture fishes in the wild, but residents of Mesopotamia constructed ponds in the fertile crescent of the Tigris and Euphrates rivers to maintain regular, accessible supplies of fishes. Pliny the Elder recommended fishes as medicinal remedies for a variety of ailments. Still today, cod-liver oil and castor oil are used to relieve internal and external ailments; and in some parts of the world, otoliths, the small ear bones of fishes, are believed to prevent colic.

The quest for fishes played a large role in early exploration and settlement patterns. Access to herring in the Baltic Sea conferred prosperity upon the Hanseatic League during the twelfth century. Disputes over fishing rights and profits led to conflicts, sometimes escalating to war, that continued among European nations long after the demise of the league. By the fourteenth century, Europeans traversed the sea to fish for cod off of Iceland. They preserved the fish in dried or salted forms to supply European markets, thereby rendering it a valuable commodity, and disputes over access to cod fishing grounds sparked further wars. Cod constituted a major portion of the diet and trade base of later British colonists that explored and settled on the northeast coast of the United States. By the late 1600s, the international cod trade involved other commodities as diverse as salt, sugar, molasses, cotton, tobacco, and even slaves.

Modern fisheries

Fisheries continue to provide a vital source of food, employment, and income in many countries today. World fisheries catch increased rapidly during the 1950s and 1960s. Following the collapse of the Peruvian anchoveta fishery in the 1970s, total catches appeared to level off, but worldwide catch began growing again in the 1980s. In 2000 marine fisheries captured nearly 95 million tons, and aquaculture production added another 35 million tons of fishes that were consumed by humans in some form—most commonly as food, oil, or fertilizer. Despite the value and varied uses of fishes, relatively few species dominate the catch. In 1997 marine fisheries exploited 186 species, but seven species accounted for 50% of the total biomass harvested.

A variety of gear types are used to catch fishes in modern commercial endeavors. Trawls (nets) may be towed along the ocean bottom to target demersal fish (bottom-dwellers) such



Fishery centers—catches are given in millions of tons (numbers from 2000). (Map by XNR Productions. Courtesy of Gale.)

as cod, or suspended in the water column to catch pelagic species such as herring. Purse seines surround migratory schools of fishes such as tuna. And hooks on long lines—baited lines stretched sometimes for miles through the water column—capture large predatory species, including sharks and swordfish. A variety of diverse techniques are utilized by many people throughout the world to harvest fishes for subsistence or local consumption. Much fishing occurs near shore using traps, nets, and spears. However, as fish populations are depleted, particularly in areas with few alternative sources of protein, humans resort to small mesh nets or destructive fishing techniques, including dynamite fishing, to capture as many remaining fishes as possible.

Recreation

Many people throughout the world enjoy recreational activities centered around fishes. Recreational anglers pursue fishes for sport in freshwater, coastal, and deep sea settings. In the United States alone, the number of anglers is estimated at over 50 million. Many of these anglers enjoy the sport for the thrill of hooking and landing a feisty fish; since the catch is of secondary importance, anglers often release their catch to reduce mortality effects on the fish population.

Another recreational pursuit involving fishes is that of maintaining aquariums. The idea of the aquarium was first developed in the mid-1800s, and the first public aquarium opened at the London Zoological Gardens in 1846. Today, the keeping and breeding of ornamental fishes is a popular hobby worldwide. Many individuals maintain smaller, personal aquariums, ranging from a single goldfish in a bowl to elaborate tropical marine tanks. This activity was the third most popular hobby in the United States in 2001. Worldwide, it generates millions of dollars of economic activity.

Conservation of fishes

Despite their value to our society, fishes suffer the direct and indirect consequences of human actions. Habitat alteration including inadequate water supplies and declining water quality, overharvesting, and introduced species all threaten the viability of fish populations. Over time, many humans have recognized the negative impacts of certain actions and initiated efforts to ameliorate the consequences of these activities.

Habitat alteration

Human actions alter fish habitats in a variety of ways, often resulting in the decline of fish populations. Dredging of channels and clearing of debris to maintain navigation in waterways removes substrates and rich food sources that fishes prefer. In addition, the loss of wetlands eliminates spawning and nursery habitats for numerous fish species. In some cases, wetlands are destroyed to create urban living space or agricultural land; in other instances, tapping into groundwater supplies lowers the water table so that wetlands are no longer inundated. While hydroelectric power provides energy to many areas, the construction of dams across rivers substantially alters the nature of flowing-water habitats and limits upstream migrations of fishes. Upstream of the dam, the river essentially becomes a lake, and dam operations control downstream water flows. Further, despite the fact that most large dams are now equipped with fish ladders to facilitate upstream migrations, significant declines in the populations of many fish species are commonly noted following dam construction. Indirect human effects on fish habitat are also important. In many tropical regions, deforestation can destroy a watershed's ability to store seasonal rainfall and release it slowly over an extended period of time. Such alterations to hydrological patterns can induce extreme cycles of flood and drought in streams that result in catastrophic consequences for the local fish fauna.

Humans consume large amounts of water for drinking and irrigation, and much of the water used is obtained from rivers and lakes inhabited by fishes. In many regions, reservoirs of dams offer convenient holding areas from which water can be withdrawn for human uses. In other settings, streams and rivers are diverted to cities for human consumption or to agricultural areas for irrigation. Either scenario results in less water to maintain natural flow patterns in rivers and streams; thus, the flooded habitat area available to fishes shrinks, many species move out of the area or become locally extinct, and

Not only do we like to watch fish swim, we sometimes join them underwater. Here, a diver swims with a lemon shark (*Negaprion brevirostris*). (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

An appetizer plate holds three kinds of caviar: golden whitefish, keta salmon, and American sturgeon. (Photo by Macduff Everton/Corbis. Reproduced by permission.)

others suffer mortality from crowding and disease. The dramatic collapse of the Aral Sea ecosystem after two major tributaries were tapped for agricultural irrigation in the 1980s demonstrates the potential consequences of water diversion on aquatic systems and their fish faunas. This problem is exacerbated in areas that draw their water from underground aquifers. Water held in aquifers is often extracted at rates that exceed natural replenishment. Mining these aquifers for human use can lower the water table sufficiently to completely eliminate aquatic habitats that are dependent on artesian spring flows, a situation of particular concern in arid regions of the southwestern United States and northern Mexico. As water shortages become more prevalent throughout the world and the human demand for water escalates, the severity of threats to fish populations will likely increase, and decisions concerning the allocation of water will become more complex and contentious.

In addition to concerns about water quantity, declining water quality also has serious implications for fishes. Humans have dumped industrial wastes, agricultural chemicals, and sewage directly into water bodies for much of history, and similar discharges continue in many areas today. Indirect runoff further reduces water quality. For example, deforestation increases siltation in adjacent streams, and nutrient runoff from the watershed may cause algal blooms in the receiving lake. These activities all impair water in ways that may be harmful to fishes. Waste effluents contribute to disease; chemicals may prove toxic or impair reproductive success; and algal blooms and the decay of materials may deplete oxygen to inadequate levels for sustaining fish life.

Overfishing

Overfishing poses another substantial threat to fish populations worldwide. The pattern noted in the history of many fisheries involves discovery, high levels of exploitation until the stock collapses, and then switching to a new stock. Even in classical times, stock collapses due to overfishing were common, and as early as the twelfth century, Edward II banned the use of a specific type of trawl net in the Thames Estuary. In recent years, we have witnessed the collapse of major fisheries, including those for Peruvian anchoveta, California sardine, and Georges Bank cod. The failure of California sardine and Atlantic cod populations to recover demonstrates that intense fishing may deplete stocks to a point that the surviving population may not be large enough to assure recovery, even if fishing effort is eliminated entirely. In addition to the demise of exploited stocks, overfishing may have consequences at the ecosystem level as well. Fishing activities may destroy habitat if inappropriate fishing gear or techniques are utilized. Further, it has been suggested that as humans deplete stocks at high trophic levels, we move to species lower on the food chain; over time, this pattern of "fishing down the food web" threatens collapse of the whole ecosystem.

Introduced species

Finally, human actions affect fish populations and communities by introducing certain species to areas beyond their native range. In many cases, the introduction to a new environment frees a species from natural controls on its population growth. The introduced species may prey upon native fishes, infringe upon habitats and food supplies used by other species, hybridize with native species and reduce genetic diversity of the stocks, or act as vectors of exotic pathogens and parasites to which native species have no resistance. Some introductions are intentional and others accidental, but both may result in severe consequences to native fish stocks. Intentional introductions often follow collapses of native fish stocks due to overexploitation. As an example, the Nile perch (*Lates niloticus*) was introduced into Lake Victoria to expand protein production and enhance fisheries after the demise of an endemic tilapia, the ngege (*Oreochromis esculentus*), due to overfishing. Over three decades, predation by Nile perch resulted in the loss of up to 70% of species in the diverse flock of haplochromine cichlids that evolved in the lake.

Status and future of fishes

The human actions described above may result in fish population declines; in some cases, extinction of the species follows.

Shark fins drying on a fishing vessel. The fins are to be used for such delicacies as shark's fin soup. Federal regulators are trying to determine the impact on shark populations. (Photograph. AP/Wide World Photos. Reproduced by permission.)

As of 2002, 115 distinct species and subspecies of fishes were protected by the U. S. Endangered Species Act, and many other species are threatened or endangered in countries throughout the world. Despite the protection afforded to these species, over 40 species have already been lost to extinction in North America alone since the early 1900s. Estimates suggest that approximately 20% of all freshwater fish species are in serious decline or already extinct. Relatively few marine species are considered at risk of extinction, despite high levels of utilization of these stocks in fisheries. The much higher threat to freshwater fishes likely reflects their utilization of restricted habitats that are intertwined with land-based human populations. It is likely that even higher numbers of species are threatened in many tropical countries due to the rich species diversity and small geographical ranges of many species.

Despite the diversity and immensity of the threats identified above, many people now recognize the negative consequences of environmental decisions and actions. Thus, efforts have been initiated to mitigate impacts to fish species and populations. Local activities often include the rearing of fishes in hatcheries to supplement wild stocks and restoration of habitat areas that have been degraded by human activities. Other efforts involve a broader group of people and often require government mandates. Such endeavors include setting aside reserves to preserve highly diverse areas, protecting critical habitats of threatened species, and developing regulations to reduce overfishing and pollution. Internationally, countries have adopted several treaties that advance conservation of fishes and their habitats, including the Convention on Biological Diversity, the Ramsar Convention on Wetlands, and the Convention on International Trade in Endangered Species (CITES). Locally and globally, it seems that we are beginning to recognize that the futures of fishes and of humans may be closely linked.

Resources

Books

Committee on Ecosystem Management for Sustainable Marine Fisheries, Ocean Studies Board, Commission on Geosciences, Environment, and Resources, National Research Council. *Sustaining Marine Fisheries.* Washington, DC: National Academy Press, 1999.

Committee on Protection and Management of Pacific Northwest Anadromous Salmonids, Board on Environmental Studies and Toxicology, Commission on Life Sciences. *Upstream: Salmon and Society in the Pacific Northwest.* Washington, DC: National Academy Press, 1996.

Dobson, Mike, and Chris Frid. *Ecology of Aquatic Systems.* Essex, England: Addison Wesley Longman, 1998.

Helfman, Gene S., Bruce B. Collette, and Douglas E. Facey. *The Diversity of Fishes.* Malden, MA: Blackwell Science, 1997.

Kurlansky, Mark. *Cod: A Biography of the Fish that Changed the World.* New York: Walker and Company, 1997.

McGinn, Nature A., ed. *Fisheries in a Changing Climate: Proceedings of the Sea Grant Symposium Held at Phoenix, Arizona, USA, 20–21 August 2001.* Bethesda, MD: American Fisheries Society, 2002.

Periodicals

Pauly, Daniel, Villy Christensen, Johanne Dalsgaard, Rainer Froese, and Francisco Torres Jr. "Fishing Down Marine Food Webs" *Science* 279 (1998): 860–863.

Organizations

American Fisheries Society. 5410 Grosvenor Lane, Bethesda, MD 20814 USA. Phone: (301) 897-8616. Fax: (301) 897-8096. E-mail: main@fisheries.org
Web site: <http://www.fisheries.org>

American Sportfishing Association. 225 Reinekers Lane, Suite 420, Alexandria, VA 22314 USA. Phone: (703) 519-9691. Fax: (703) 519-1872. E-mail: info@asafishing.org
Web site: <http://www.asafishing.org>

Other

Food and Agricultural Organization of the United Nations. "FAO Fisheries" (cited 5 February 2003). <http://www.fao.org/fi/default.asp>

Katherine E. Mills, MS

Myxiniformes
(Hagfishes)

Class Myxini
Order Myxiniformes
Number of families 1

Photo: A Pacific hagfish (*Eptatretus stoutii*) with secreted slime. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Modern vertebrates are classified into two major groups, the Gnathostomes (jawed vertebrates) and the Agnathans (jawless vertebrates). The Agnathans are classified into two groups, myxinoids (hagfishes) and petromyzonids (lampreys). The Gnathostomes constitute all the other living vertebrates, including the bony and cartilaginous fishes and the tetrapods. The hagfishes are considered the most primitive vertebrates known, living or extinct.

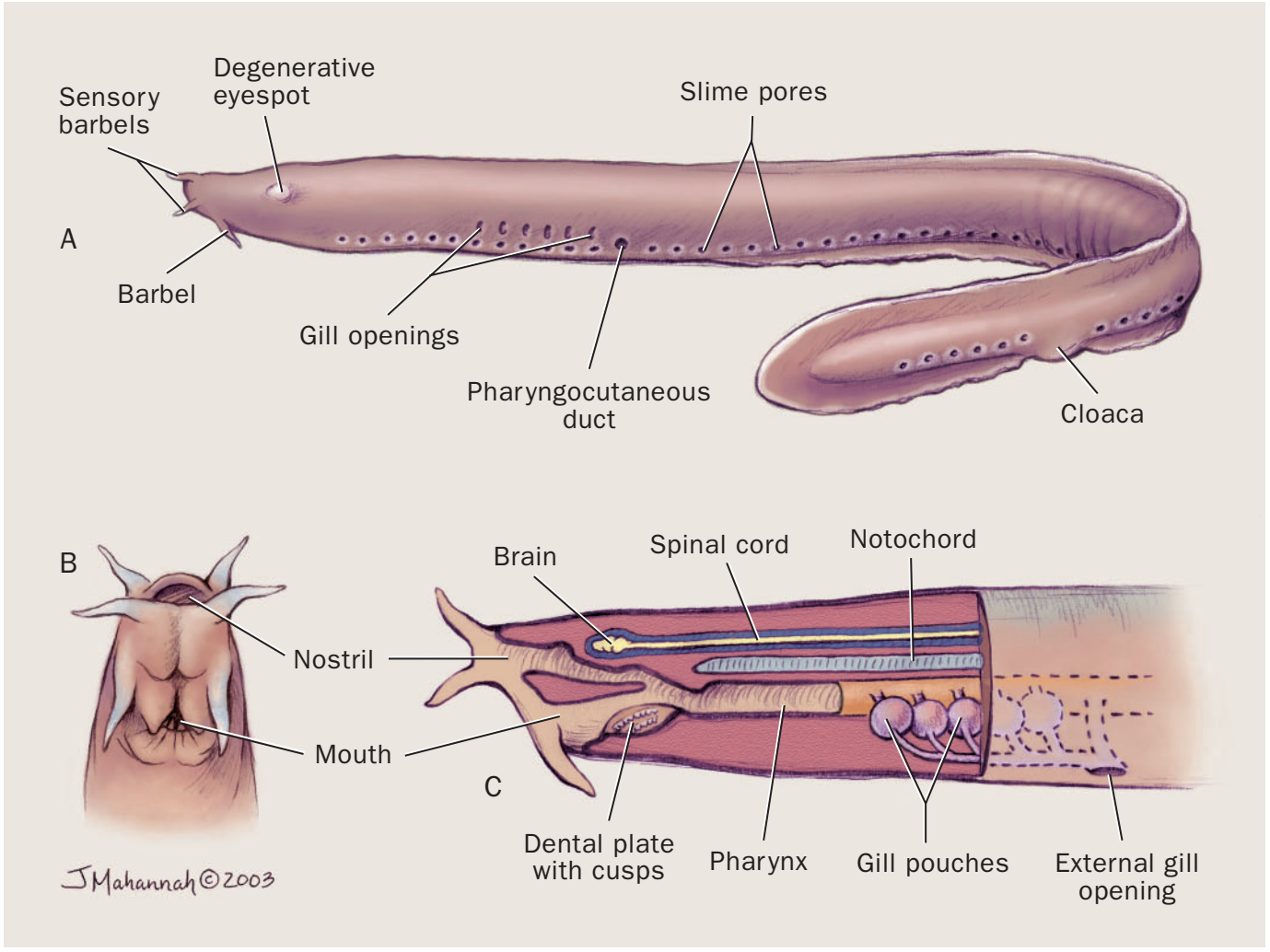
Hagfishes are members of the family Myxinidae, which is the only surviving family of the class Pteraspidomorphi. The species are divided into two primary genera: *Eptatretus* and *Myxine*. The genus *Eptatretus* (found in the Pacific Ocean) has 37 species; the genus *Myxine* (found in the Atlantic Ocean) has approximately 18 species.

Hagfishes are the products of a long evolutionary history and can be considered as primitive, specialized, and degenerative. The hagfish lineage extends over 530 million years and is clearly monophyletic in its origin. Hagfishes are the oldest lineage of vertebrates and are thus very important to evolutionary studies. However, hagfishes are not well represented in the fossil record due to their lack of bony structures. The fossil record consists of a single fossil representing one species of one genus, *Myxinikela siroka*. The discovery of this fossilized hagfish, in sediments deposited roughly 330 million years ago, put the significance of the hagfishes into new light. The hagfishes are an important link between invertebrates and vertebrates, and thus are of interest to evolutionary biologists in regard to both their anatomy and physiology, because they may retain characteristics of ancestral extinct species that are common to their closest relatives, the primitive fossil fishes.

Physical characteristics

All hagfish species have a cartilaginous skeleton with no vertebrae, true fin rays, paired fins, or scales. Hagfishes lack jaws, but have two laterally biting dental plates with keratinous cusps. The mouth is an oval slit, with four fleshy barbels, and a strong tooth on the tongue. The single nostril is surrounded by another four sensory barbels that allow the hagfish to acutely scent food. The eyes of the Pacific hagfishes (*Eptatretus stoutii*) exist as degenerative eyespots covered with thick skin. Atlantic hagfishes (*Myxine glutinosa*) have more degenerative eyespots than Pacific hagfishes. Atlantic hagfishes range in size between 17.7–23.6 in (45–60 cm), but not exceeding 30.7 in (78 cm), in length. Pacific hagfishes are slightly smaller, not exceeding 25.6 in (65 cm) in length. Hagfishes have six to 10 pairs of internal gill pouches, which may open separately to the exterior or unite to form a single exterior opening on each side of the animal, depending on the species. In Pacific hagfishes, short efferent ducts lead to 10–14 external gill openings; in Atlantic hagfishes the efferent ducts discharge through a common external opening. Color ranges from reddish brown to grayish pink.

One interesting feature of the hagfishes that is unique among other fishes or vertebrates is the production of copious quantities of slime. Hagfishes have approximately 150 to 200 slime glands along the side of the body. When a hagfish is attacked or handled, it will secrete small amounts of slime. When the slime comes in contact with the surrounding seawater, the mucous component of the slime expands greatly as it is hydrated with the water, increasing its volume several fold. In order for the hagfish to rid itself of the slime, it literally ties itself in a knot and scrapes itself clean by moving the knot down the body. The slime is used as a defense mechanism and may be involved in reproduction.



A. External anatomy of hagfish subfamily Eptatretinae; each gill pouch has a separate opening to the exterior. B. Ventral view of closed mouth and single nasal opening. C. Anterior section of subfamily Myxininae; gill pouches have a single common external opening on each side. (Illustration by Jacqueline Mahannah)

Distribution

Hagfishes have been reported from the Atlantic, Pacific, Indian, Arctic, and Antarctic Oceans, and from the Bering, Mediterranean, and Caribbean Seas. Hagfishes do not occur in the Red Sea or the Gulf of Thailand. Atlantic hagfishes are found on both sides of the North Atlantic and in Arctic Seas in deep water of 3,937–11,811 ft (100–300 m) on soft muddy bottoms. Their distribution is varied and patchy, being confined to areas with a suitable bottom. Pacific hagfishes are found along the Pacific coast of North America, from southern California to southeast Alaska. They are found on diverse substrates from muddy bottoms to sand/gravel and boulder/ sand substrates.

Habitat

Hagfishes mostly inhabit deep marine environments that are relatively free of circadian or seasonal changes. Temperature and salinity are thought to be two of the most important factors to influence hagfish distribution. The fishes are most often found in waters that are cooler than 71.6°F (22°C) and have salinities between 32–34 parts per thousand. Although they are most commonly found at the bottom of the ocean—the deepest reported hagfish sighting was 196,850 ft (5,000 m)—some species have been reported in depths as shallow as 394 ft (10 m). Pacific hagfishes occupy a wider range of substrate types than Atlantic hagfishes. Pacific hagfishes occur on substrates ranging from soft muddy bottoms to boulder/sand substrates, and are often found in a coiled position nestled among the rocks. Atlantic hagfishes are most often found on soft muddy substrates in which they form burrows. Atlantic hagfishes burrow by first orienting the body in a vertical position above the substrate and then swimming head first into the substrate. Once the anterior half is below the surface of the mud, the anterior portion pulls the posterior portion below the surface.

Hagfishes are an important part of the benthic marine environment. They are a substantial proportion of the benthic biomass; are critical for substrate turnover and the clean-up and processing of carrion falls; they prey on benthic inverte-

brates as well as provide prey for marine mammals and large predatory invertebrates.

Behavior

The Japanese hagfish (*Eptatretus burgeri*) is the only known species that undertakes an annual migration, which is thought to be associated with the reproductive cycle.

Feeding ecology and diet

Hagfishes are chiefly scavengers and feed on crustaceans, small marine worms, and vertebrate remains. Using its strong teeth, the hagfish pierces the fish's skin and bores into the body, eating the flesh and eventually only leaving the bone and skin. Gut analyses of Atlantic hagfishes have shown a diet consisting primarily of invertebrate organisms, including polychaetes, hermit crabs, and shrimps.

The Atlantic hagfish has few known predators. Small hagfish have been found in the stomachs of codfish, harbour porpoise, octopus, Peale's dolphin, and sea lions. Hagfish eggs have also been found in the stomachs of male hagfish.

Reproductive biology

The reproductive patterns of most hagfishes are unknown. Females produce a small number (20–30) of large yolky eggs 0.8–1 in (20–26 mm) long. The eggs are enclosed in a tough shell with threads at each end, which act as anchors in the mud. Males produce a small amount of sperm. As neither sex has a copulatory organ, the mode of fertilization is thought to be external.

Sex is often difficult to determine in hagfishes. Atlantic hagfishes have been considered functional hermaphrodites, with their single unpaired sex organ developing sperm in the posterior portion and eggs later in the anterior portion. Other investigations have shown that hagfishes are not hermaphrodites, but that the gonads undergo differentiation into male and female gonads. More recent studies suggest that Atlantic hagfishes could indeed function as hermaphrodites for part of their life cycle, reproducing as either male or female at other times.

The spawning behavior and frequency is unknown. The Japanese hagfish appears to have an annual reproductive cycle associated with its migration into deep waters. At least two species of hagfishes spawn throughout the year, for ripe Atlantic hagfish females and those nearing ripeness have been recorded during all seasons.

It has been noted that Pacific hagfish females in an aquaria ceased to feed when they approached sexual maturity, as do many other fishes. Hagfishes lay their eggs in clutches, strongly supporting evidence that hagfishes do not die after spawning. Although there are no documented answers as to how hagfishes reproduce, considerable data have led to the following conclusions: reproduction takes place at a depth in excess of 164 ft (50 m), there is no marked season of sexual activity (except in the Japanese hagfish), and the eggs are fertilized externally and anchor themselves by their hooks not far from where they were extruded. The last fertilized hagfish eggs reported were obtained by Julia Worthington in 1903.

Conservation status

No species are listed on the IUCN Red List. During the past 40 years, hagfishes have constituted a valuable fishery off the coasts of Japan and Korea, for both meat and skins. A commercial fishery for hagfishes begin in 1987 on the West Coast of the United States, and moved to the East Coast in early 1992 when catches on the West began to decline. There are currently few regulations on the commercial hagfish industry in the United States. Catches from the Gulf of Maine have increased steadily since the mid 1990s, as the Atlantic hagfishes were targeted by U.S. and Canadian fishermen to meet the South Korean demand for "eel" skin, used to manufacture leather goods. Since the fishery began along the New England coast there has been an apparent decline in the number of hagfishes caught in the nearshore fishery.

Significance to humans

Atlantic hagfishes are considered an important species in the Gulf of Maine because they play a significant role in the benthic ecosystem throughout the gulf; have both important direct and indirect effects on commercial fisheries in the gulf, consuming by-catch and providing food; and are targeted by U.S. and Canadian fishers to meet the South Korean demand for "eel" skin. It is likely that all hagfishes have a crucial and significant role in the benthic ocean ecosystem, and the loss of hagfishes could have a major impact on nutrient recycling in the world's oceans.

Species accounts

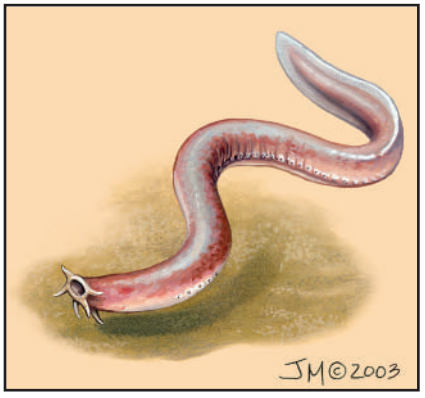
Atlantic hagfish
Myxine glutinosa

FAMILY
Myxinidae

TAXONOMY
Myxine glutinosa Linnaeus, 1785, Europe; Mediterranean to Murmansk.

OTHER COMMON NAMES
English: Slime eel.

PHYSICAL CHARACTERISTICS
Between 17.7–23.6 in (45–60 cm) in length, but not exceeding 30.7 in (78 cm). Jawless, single nasal opening, single pair of external gill openings, degenerative eyespots covered with thick skin. Grayish or reddish brown.



Myxine glutinosa

DISTRIBUTION
Widely distributed in European seas from Murmansk to Mediterranean Sea. Absent in eastern Mediterranean and Black Seas. Present in northwest Atlantic.

HABITAT
Deep waters of 328–984 ft (100–300 m) on soft muddy substrates in which they form burrows.

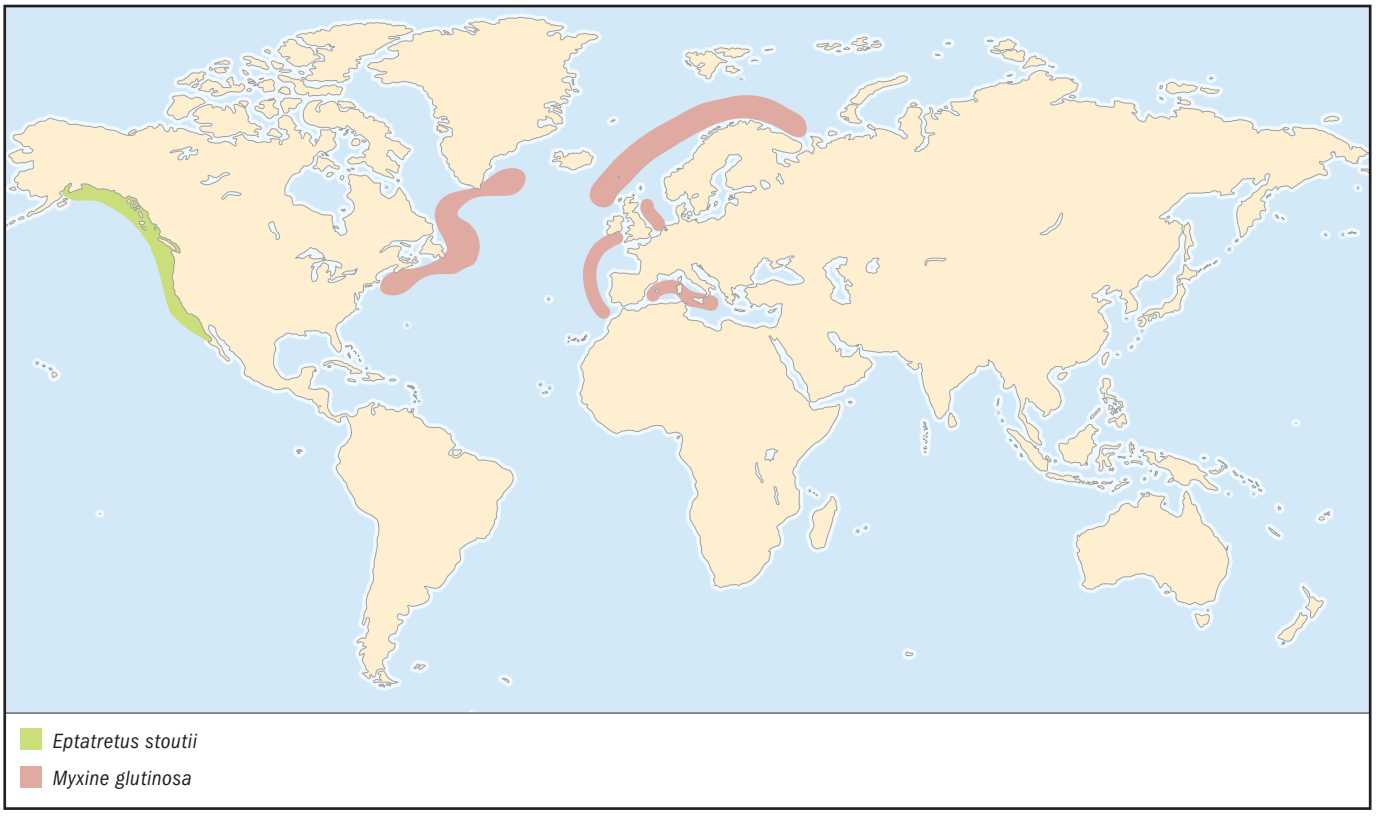
BEHAVIOR
Burrows by first orienting the body in a vertical position above the substrate and then swimming head first into the substrate. Once the anterior half is below surface of the mud, the posterior portion is pulled below the surface by the anterior, leaving only the nasal opening extruding above the mud.

FEEDING ECOLOGY AND DIET
Feeds on dead and dying fishes, crustaceans, and other small benthic organisms.

REPRODUCTIVE BIOLOGY
Females produce 20–30 large yolky eggs. Fertilization is thought to be external, but has never been observed. It is not known if there is a seasonal reproductive cycle.

CONSERVATION STATUS
Not listed as a threatened or endangered, but fishermen have reported reduced catches in recent years in the Gulf of Maine.

SIGNIFICANCE TO HUMANS
Hagfish skin is processed into various leather goods and marketed as "eel" skin. ◆



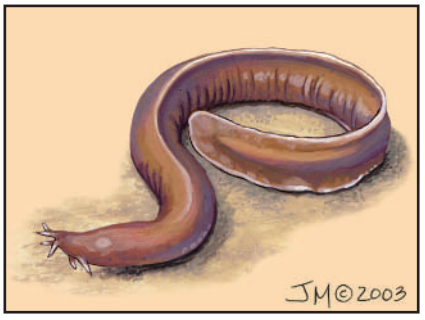
Pacific hagfish
Eptatretus stoutii

FAMILY
Myxinidae

TAXONOMY
Bdellostoma stoutii Lockington, 1878, West Coast of North America, South China Sea, Philippines.

OTHER COMMON NAMES
English: Slime eel.

PHYSICAL CHARACTERISTICS
Does not generally exceed 25.6 in (65 cm) in length. Jawless, single nasal opening; 10–14 gill pouches open directly to external gill openings. Dark brown, tan, gray, or brownish red, often tinted with blue or purple, never black, lighter ventrally, rarely with large patches of white. Eyes exist as degenerative eye spots covered with thick skin.



Eptatretus stoutii

DISTRIBUTION
Widely distributed in the Eastern Pacific: southeastern Alaska to central Baja California, Mexico.

HABITAT
Occupies a wider range of substrate types than Atlantic hagfishes. Occurs at over 330 ft (100 m) on substrates ranging from soft muddy bottoms to boulder/sand substrates.

BEHAVIOR
Burrows in soft sediments and is often found in a coiled position nestled among rocks in boulder/gravel substrates.

FEEDING ECOLOGY AND DIET
Feeds on dead and dying fishes, crustaceans, and other small benthic organisms.

REPRODUCTIVE BIOLOGY
Females produce 20–30 large yolky eggs. fertilization is thought to be external, but has never been observed. it is not known if there is a seasonal reproductive cycle.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hagfish skin is processed into various leather goods and marketed as "eel" skin. ◆

Resources

Books

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Petromyzoniformes
(Lampreys)

Class Cephalaspidomorphi
Order Petromyzoniformes
Number of families 3

Photo: A sea lamprey (*Petromyzon marinus*) feeding on a fish. (Photo by Berthoula-Scott/Jacana/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Modern vertebrates are classified into two major groups, the Agnathans (jawless vertebrates) and the Gnathostomes (jawed vertebrates). The Agnathans are classified into two groups, myxinoids (hagfishes) and petromyzonids (lampreys). The Gnathostomes include all other living vertebrates, including the bony and cartilaginous fishes and the tetrapods.

There are approximately 40 species of lampreys, which belong to the order of Petromyzoniformes. This order is divided into three families: the Petromyzonidae, the Northern Hemisphere lampreys (also referred to as the Holarctic species), and the two Southern Hemisphere families, Geotriidae and Mordaciidae. The Petromyzonidae consists of six genera: *Ichthyomyzon*, *Petromyzon*, *Caspiomyzon*, *Eudontomyzon*, *Tetrapleurodon*, and the *Lampetra*. The genus *Lampetra* is further divided into three subgenera: *Entosphenus*, *Lethenteron*, and *Lampetra*. The Geotriidae and Mordaciidae each consist of only one genus, *Geotria* and *Mordacia*, respectively.

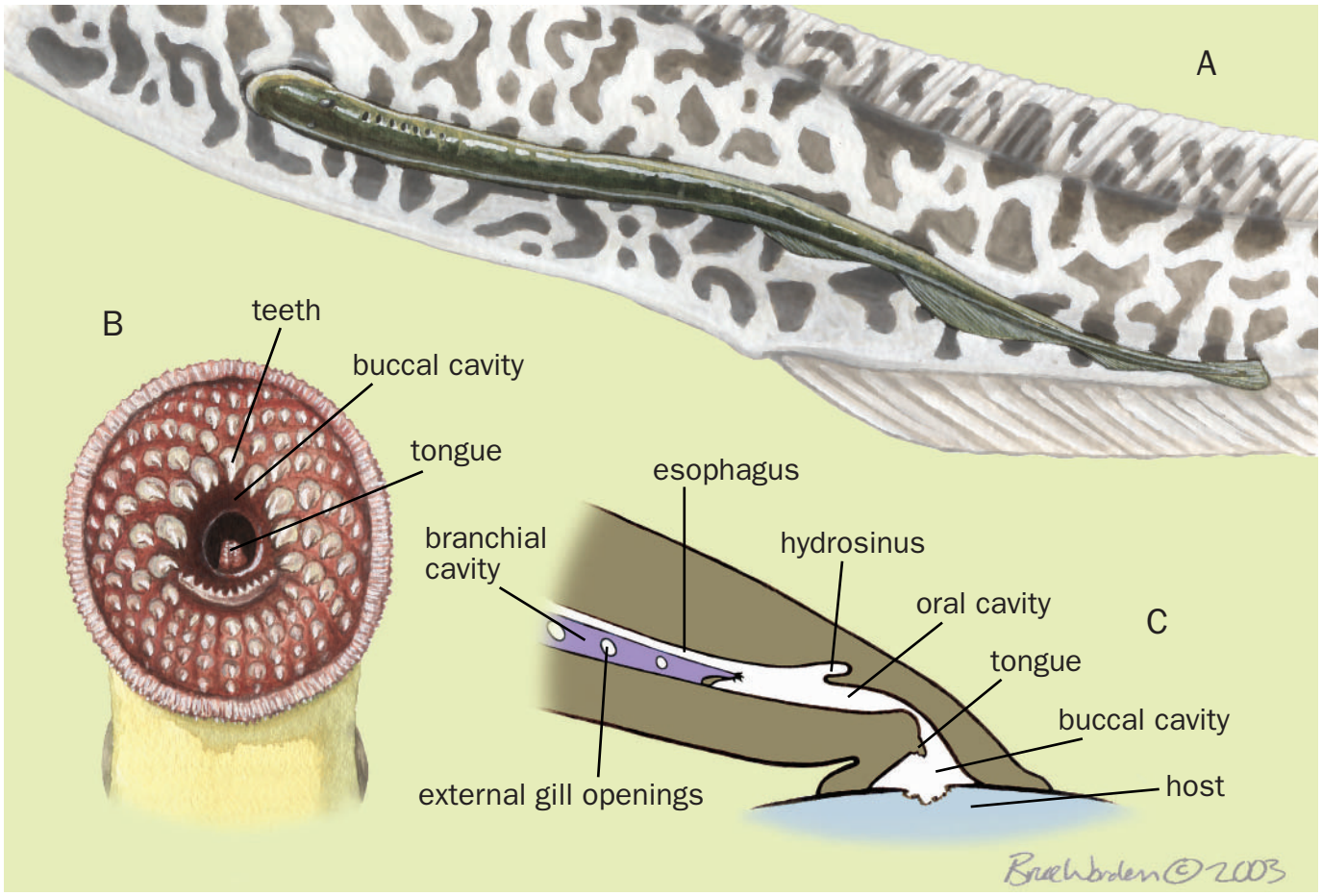
The phylogeny of lampreys is based primarily on dentition and is justified by other shared anatomical traits, such as the proportional measurements of body parts, size of the adult, snout shape, eyes, and dorsal fins. The species of *Ichthyomyzon* are thought to be the most ancient of the lampreys because their simple teeth are arranged into rows throughout the entire oral disc. Of these species, the silver lamprey (*I. unicuspis*) is considered the most primitive.

Lampreys are representatives of the oldest lineage of vertebrates, the Agnathans. The agnathans probably arose as the first vertebrates about 550 million years ago, immediately after the evolutionary explosion of multicellular organisms in the Cambrian period. Paleontological analysis of extinct agnathans suggests that lampreys are more closely related to gnathostomes (the jawed vertebrates) than either group is to the hagfishes, although recent molecular analysis groups the hagfishes together with the lampreys in a single clade. Definite fossil records date back to the Upper Carboniferous, about 280 million years ago. Like hagfishes, lampreys are an important linkage between invertebrates and vertebrates and thus their anatomy and physiology are of interest to evolutionary biologists because they may retain characteristics of ancestral extinct species that are common to their closest relatives, the primitive fossil fishes.

Physical characteristics

Lampreys are scaleless, eel-like fishes that have skeletons of cartilage instead of bone. They have a notochord, but lack vertebrae. They also lack true fin rays and paired fins, but have one to two dorsal fins. Lampreys lack jaws but have teeth on the oral disc and tongue. Adult lampreys range in length from 7.9 in to 47.2 in (20 to 120 cm).

Lamprey species may be parasitic or nonparasitic. With a few exceptions, the nonparasitic species appear, based on characters and distribution, to have evolved from an extant parasitic lamprey. The four species of lampreys described in this chapter are parasitic lampreys: the sea lamprey (*Petromyzon marinus*), the silver lamprey (*I. unicuspis*), the pouched lamprey (*Geotria australis*), and the short-headed lamprey (*Mordacia mordax*). The sea lamprey and silver lamprey belong to the Northern Hemisphere family; the pouched lamprey and short-headed lamprey belong to the Southern Hemisphere family. Members of Petromyzonidae have the highest number of chromosomes (164–174) among vertebrates. Adult lampreys are distinct in their sex, either male or female. Lampreys spawn only once in their lifetime, after which they die. Parasitic lampreys are generally anadromous.



A. Sea lamprey (*Petromyzon marinus*) feeds on a host fish; B. Mouth of *P. marinus*; C. Sagittal section of *P. marinus* attached to host. (Illustration by Bruce Worden)

Distribution

Lampreys occur mainly in temperate zones. Parasitic species are generally of one of two types: those that are anadromous and feed at sea, and those that are restricted to river systems. There is little information on the marine distribution of anadromous species, although it is thought that the larger species move farther away from the coastline than the smaller species. The larger species may in turn give rise to forms that feed in lakes, such as the landlocked sea lamprey of the Great Lakes. Nonparasitic species are restricted to fresh water, most commonly to creeks and smaller rivers. The sea lamprey is found in coastal waters on both sides of the North Atlantic and in the western Mediterranean, and also in fresh waters of the Atlantic coasts of Europe and North America. The landlocked sea lamprey is found in the Great Lakes of North America. The silver lamprey is found in and around the states and provinces of the Great Lakes region. The distribution records of Southern Hemisphere lampreys are less well known due to lack of systematic investigations, but it is known that the pouched lamprey occurs in New Zealand, Western Australia, and Tasmania, and on both coasts of South America; the short-headed lamprey occurs only in southeast Australia and Tasmania.

Habitat

Larval lampreys are wormlike filter-feeding fishes that bury in the sand or mud of rivers. Toward the end of the larval phase, lampreys undergo an extensive metamorphosis in which they become free swimming and migrate to oceans or lakes, where they become parasitic. After one to three years in the parasitic phase, lampreys return to freshwater streams with sand, gravel or pebble substrates to spawn.

Behavior

Lampreys spawn only once in their lifetime, after which they die. The parasitic lampreys begin their lives as freshwater ammocoetes (larval lampreys), which are blind, filter-feeding larvae. After approximately three to seven years in freshwater streams, metamorphosis occurs, and the ammocoetes become free-swimming, sexually immature lampreys, which migrate to the sea or lakes. The actual time for the parasitic phase is not known for all species, but is generally thought to be one to two years. After this period, lampreys return to freshwater streams and undergo the final maturational processes resulting in mature eggs and sperm. The lampreys carry out specific spawning behaviors, including nest building and fanning behavior, after

A sea lamprey (*Petromyzon marinus*) showing underside of sucker-disc mouth. (Photo by Animals Animals ©Zig Leszczynski. Reproduced by permission.)

which they die. Prior to metamorphosis, the parasitic and nonparasitic lampreys are indistinguishable. After metamorphosis, the two are distinguished based on size, feeding behavior, and gonad structure, among other traits.

Feeding ecology and diet

During their larval phase, lampreys feed on microscopic plankton, algae and detritus filtered from the mud. During the parasitic phase, they attach to a host fish and extract the blood and/or muscle tissue. Lampreys do not feed in the final spawning phase. Natural predators of the nonparasitic and immature parasitic lampreys include a variety of species of fishes (e.g., eel sand trout) and birds (e.g., gulls).

Reproductive biology

The gonad in both sexes of lamprey sexes is unpaired and median, and is suspended from the dorsal wall of the body cavity by means of a mesentery containing connective tissue. Lampreys are among the few vertebrates, including teleost fishes, that have no intraperitoneal genital ducts. After hatching, for periods varying from six months to over two years in the larval phase, the undifferentiated gonad shows comparatively little further development. Throughout this stage, the germ cells divide only slowly, if at all, remaining solitary or arranged in small groups of slightly advanced cells. After this period, these cells continue to develop into primary oocytes, which occur in all ammocoete gonads regardless whether the lamprey is to become a male or female. Just before metamorphosis, the lampreys undergo sexual differentiation. In lampreys destined to become females, the gonad will continue with the process of oogenesis. In males, the oocytes undergo degeneration and atresia, and the remaining germ cells develop into nests of primary spermatogonia either shortly before, or during, metamorphosis. In the parasitic sea lamprey, sexual maturation is a seasonal, synchronized process. During the parasitic sea phase, which lasts for approximately one to three years, the development of the gametes progresses. In males, spermatogonia proliferate and develop into primary and secondary spermatocytes; in females, vitellogenesis occurs. After this period, lampreys return to freshwater streams and undergo the final maturational processes that result in mature eggs and sperm, and finally spawn, after which the lampreys die. Both sexes of lampreys develop secondary sexual characters during the final weeks of reproduction and spawning activity.

Conservation status

No species of Petromyzoniformes are included on the IUCN Red List.

Significance to humans

Lampreys are important species in the ecosystems in which they reside, whether in streams as filter-feeding organisms

A sea lamprey (*Petromyzon marinus*) showing its circumeral teeth. (Photo by Gary Meszaros/Photo Researchers, Inc. Reproduced by permission.)

helping to recycle nutrients, or as food for predatory fishes and birds in streams and oceans. In certain parts of the world, such as New England in the United States, efforts are being made by state and federal agencies to maintain or increase the populations for this reason. However, in the Great Lakes Region and Lake Champlain, sea lampreys are considered a major deterrent to fish populations because of their parasitic phase, during which they feed on other fishes with their suctorial mouth, extracting body fluids, and often causing high mortalities. The extraordinary amount of damage to the fishery of the Great Lakes caused by the invasion of the sea lamprey has resulted in one of the largest and most intensive efforts to control a vertebrate predator ever attempted. The lampreys are believed to have invaded the Great Lakes beginning with the opening of the Erie Canal in 1819, and the Welland Canal in 1829, which allowed the movement of fishes from Lake Ontario into the Upper Great Lakes from the Atlantic Ocean. By the 1930s, the lampreys had established themselves in all the Great Lakes. The Great Lakes Fishery Commission (GLFC) was established in 1955 by a treaty between Canada and the United States. The two major responsibilities of this Commission were, and continue to be, to develop coordinated programs of research in the Great Lakes, and to formulate and implement programs to eradicate or minimize sea lamprey populations in the Great Lakes.

While lampreys are not presently regarded as food fishes, they were highly prized by both classical and medieval consumers of sea food.

1. Silver lamprey (*Ichthyomyzon unicuspis*); 2. Pouched lamprey (*Geotria australis*); 3. Sea lamprey (*Petromyzon marinus*); 4. Short-headed lamprey (*Mordacia mordax*). (Illustration by Emily Damstra)

Species accounts

Pouched lamprey
Geotria australis

FAMILY
Geotriidae

TAXONOMY
Geotria australis Gray, 1851.

OTHER COMMON NAMES
English: Wide-mouthed lamprey; Spanish: Anguila blanca, lamprea de bolsa.

PHYSICAL CHARACTERISTICS
Total length generally around 19.7 in (50 cm), but fishes up to 24.4 in (62 cm) have been reported. Eel-like, scaleless, lack jaws, have funnel-like mouths and cartilaginous skeletons. Grayish in color with bands of blue-green or brown, depending on stage of reproductive development. Gonad in both sexes is unpaired and median, and is suspended from the dorsal wall of the body cavity by means of a mesentery containing connective tissue.

DISTRIBUTION
Coastal waters of continents of the Southern Hemisphere; also upstream within freshwater tributaries.

HABITAT
Heads of freshwater streams in coastal areas. Lives in open waters for approximately two years, then returns to fresh waters to spawn.

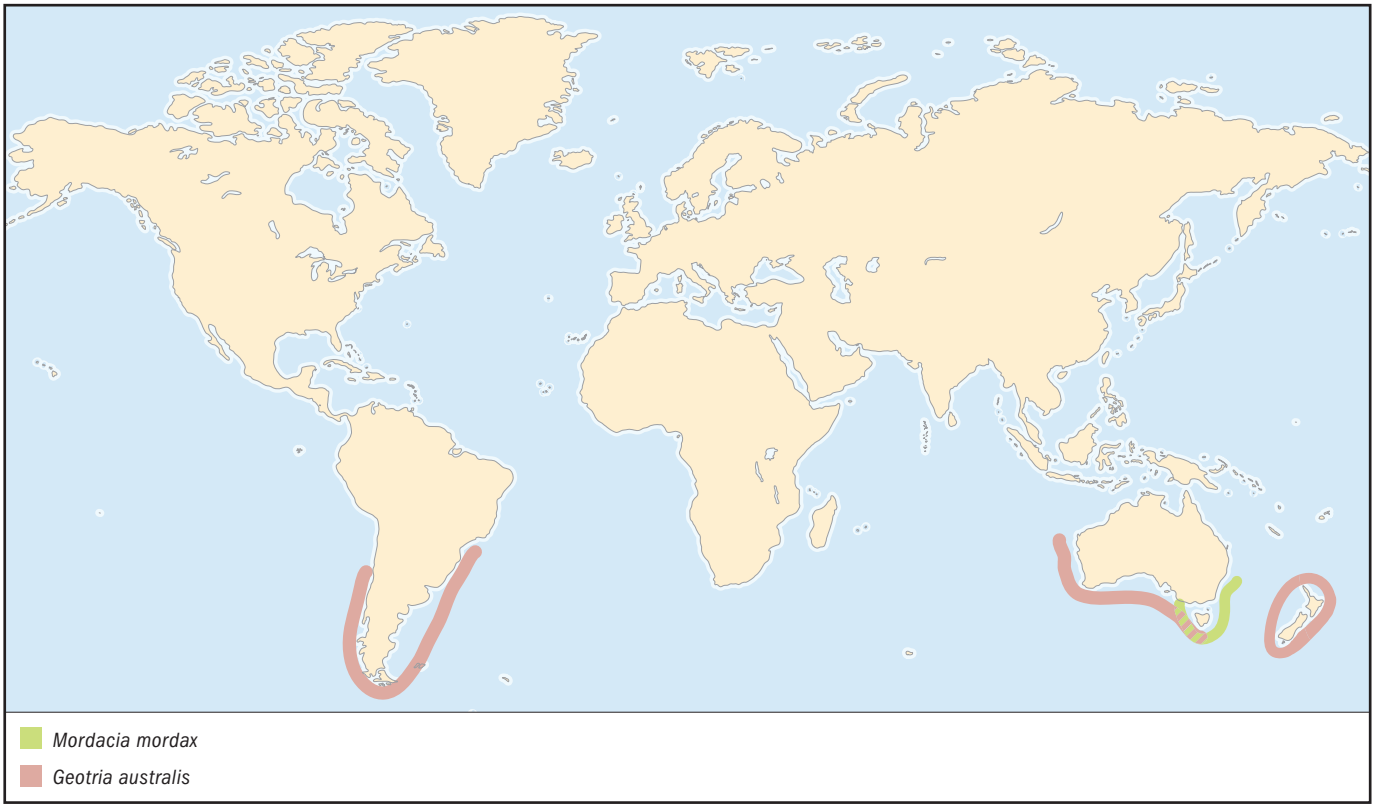
BEHAVIOR
Anadromous; returns to fresh waters to reproduce, during which time it carries out spawning behaviors, including nest building and fanning behavior.

FEEDING ECOLOGY AND DIET
Larvae feed on microscopic plankton, algae, and detritus filtered from the mud. During the parasitic phase, this lamprey attaches to a host fish and extracts blood and/or muscle tissue. Does not feed during migration upstream to spawn in fresh water.

REPRODUCTIVE BIOLOGY
The spawning run lasts for approximately 16 months and takes place during the night, particularly during heavy rains and on nights with a dark moon. The female releases her eggs, which are fertilized by released sperm from the male. The adult lampreys die shortly after spawning.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Research on this species can provide insight into human biology and perhaps yield medicinal applications. ◆



Short-headed lamprey
Mordacia mordax

FAMILY
Mordaciidae

TAXONOMY
Mordacia mordax Richardson, 1846.

OTHER COMMON NAMES
English: Australian lamprey, Murray lamprey.

PHYSICAL CHARACTERISTICS
Length generally around 20 in (50 cm). Eel-like, scaleless, lack jaws, have funnel-like mouths and cartilaginous skeletons. Body grayish brown in color, but turns blue during upstream spawning migration. The gonad in both sexes is unpaired and median, and is suspended from the dorsal wall of the body cavity by means of a mesentery containing connective tissue.

DISTRIBUTION
Coastal waters of southeastern Australia and Tasmania, as well as upstream within freshwater tributaries.

HABITAT
Heads of freshwater streams of coastal areas of southeastern Australia and Tasmania. Lives in the open waters around southeastern Australia, then returns to fresh waters to spawn.

BEHAVIOR
Anadromous; returns to fresh waters to reproduce, during which time it carries out spawning behaviors, including nest building and fanning behavior.

FEEDING ECOLOGY AND DIET
Larvae feed on microscopic plankton, algae, and detritus filtered from the mud. During the parasitic phase, adult attaches to a host fish and extracts blood and/or muscle tissue. Does not feed after migrating upstream to spawn in fresh water.

REPRODUCTIVE BIOLOGY
Female releases her eggs, which are fertilized by released sperm from the male. The adults die shortly after spawning.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Research on this species can provide insight into human biology and perhaps yield medicinal applications. ◆

Silver lamprey
Ichthyomyzon unicuspis

FAMILY
Petromyzonidae

TAXONOMY
Ichthiomyzon unicuspis Hubbs and Trautman, 1937.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length 15.3 in (39 cm). Eel-like, scaleless, lack jaws, have funnel-like mouths and cartilaginous skeletons. Body grayish brown in color. Gonad in both sexes is unpaired and median, and is suspended from the dorsal wall of the body cavity by a mesentery containing connective tissue. Considered the most primitive *Ichthyomyzon* species.

DISTRIBUTION
Hudson Bay and Great Lakes regions, as well as the St. Lawrence river system.

HABITAT
Heads of freshwater streams around the Great Lakes and Hudson Bay regions, as well as the St. Lawrence.

BEHAVIOR
Anadromous; returns to fresh waters to reproduce, during which time it carries out spawning behaviors, including nest building and fanning behavior.

FEEDING ECOLOGY AND DIET
Larvae feed on microscopic plankton, algae, and detritus filtered from mud. During the parasitic phase, adult attaches to a host fish and extracts blood and/or muscle tissue. Does not feed after migrating upstream to spawn in fresh water.

REPRODUCTIVE BIOLOGY
Female releases her eggs, which are fertilized by released sperm from the male. The adults die shortly after spawning.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Research on the species can provide insight into human biology and perhaps yield medicinal applications. ◆

Sea lamprey
Petromyzon marinus

FAMILY
Petromyzonidae

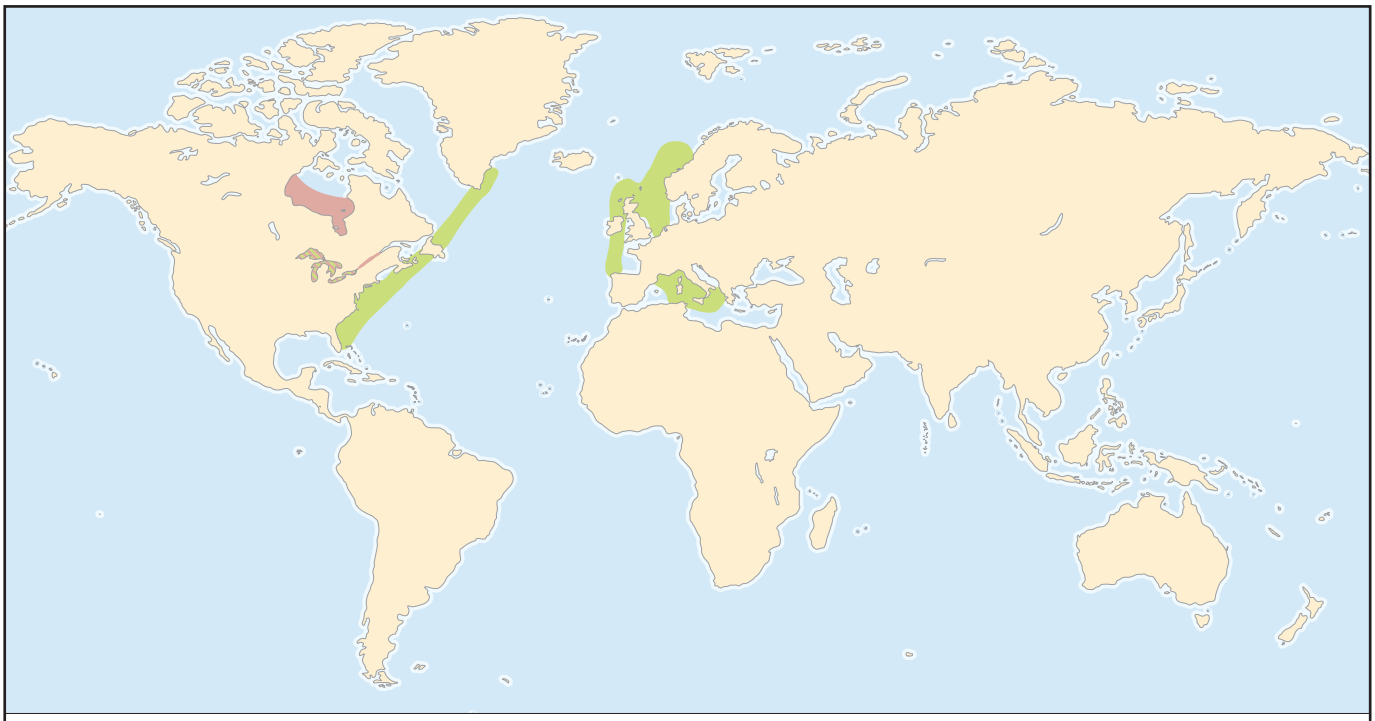
TAXONOMY
Petromyzon marinus Linnaeus, 1758.

OTHER COMMON NAMES
English: Eel sucker, Green sea lamprey, lamprey eel; French: Lamproie marine; German: Große lamprete; Spanish: Lamprea de mar.

PHYSICAL CHARACTERISTICS
Total length 47.2 in (120 cm). Eel-like, scaleless, lack jaws, have funnel-like mouths and cartilaginous skeletons. Body grayish brown in color. Gonad in both sexes is unpaired and median, and is suspended from the dorsal wall of the body cavity by a mesentery containing connective tissue.

DISTRIBUTION
Coastal waters on both sides of the North Atlantic, the western Mediterranean, also fresh waters of the Atlantic coasts of Europe and North America: landlocked in the Great Lakes of North America.

HABITAT
Immature fishes can be found in the mouths of freshwater streams of eastern North America, Northern Europe, and



western regions of the Mediterranean. Mature fishes live in the open waters of the Atlantic Ocean and Mediterranean Sea.

BEHAVIOR
Anadromous; returns to fresh waters to reproduce, during which time it carries out spawning behaviors, including nest building and fanning behavior.

FEEDING ECOLOGY AND DIET
Larvae feed on microscopic plankton, algae, and detritus filtered from mud. During the parasitic phase, adult attaches to a host fish and extracts blood and/or muscle tissue. Does not feed after migrating upstream to spawn in fresh water.

REPRODUCTIVE BIOLOGY
Female releases approximately 200,000 eggs, which are fertilized by released sperm from the male. The adults die shortly after spawning.

CONSERVATION STATUS
Not listed by the IUCN. Considered a critical species in their natural ecosystems and efforts are being made by state and federal agencies to maintain or increase populations there. In the Great Lakes, where the species has been introduced, authorities are working to control their populations because of their detrimental impact on native fishes.

SIGNIFICANCE TO HUMANS
Very destructive to fish populations in the Great Lakes Region and Lake Champlain. During the parasitic phase, feeds on other fishes with its suctorial mouth, extracting body fluids and often causing high mortalities. ◆

Resources

Books

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Chimaeriformes
(Chimaeras)

Class Chondrichthyes
Order Chimaerformes
Number of families 3

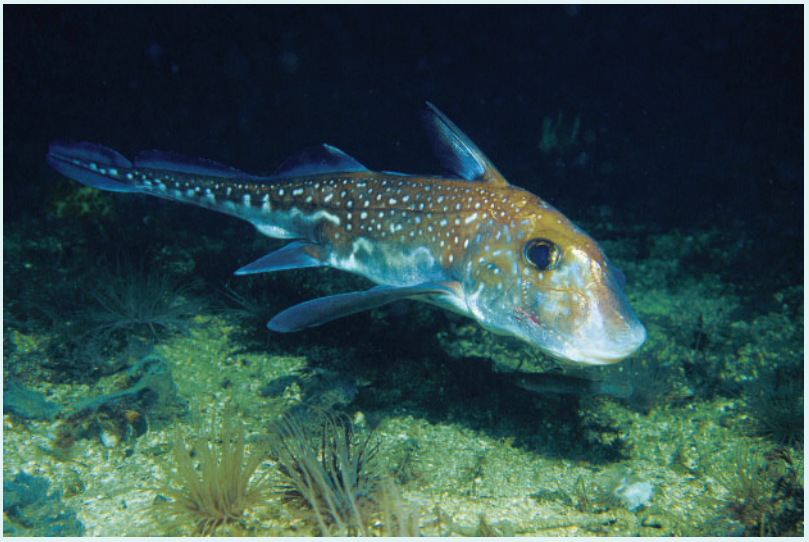


Photo: Spotted ratfish (*Hydrolagus colliei*) swim just above the sea floor and eat clams, worms, starfish, fish, and shrimp. (Photo by Brandon D. Cole/Corbis. Reproduced by permission.)

Evolution and systematics

The chimaeras are an ancient lineage of cartilaginous fishes related to sharks, skates, and rays. All chimaeras, sharks, skates, and rays are united in the class Chondrichthyes, which is further subdivided into two subclasses: Holocephali, consisting of the chimaeras characterized by a unique jaw and tooth morphology, and the Elasmobranchii, which includes the sharks, skates, and rays. Fossil evidence indicates that the chimaeras probably evolved nearly 300 million years ago. What is especially remarkable is that many of the modern forms look very much like their fossil ancestors.

Within the Order Chimaeriformes there are three families, each of which is distinguished by a unique snout morphology. The plow-nosed chimaeras of the family Callorhinchidae have a delicate flap of skin in the shape of a hoe projecting from the snout; the long-nosed chimaeras of the family Rhinochimaeridae are characterized by elongate, pointed snouts; and the ratfishes, family Chimaeridae, have blunt fleshy snouts. As of 2002 there are 33 described species of chimaeras with at least 10 additional species that are known, but not yet formally described.

Physical characteristics

Chimaeras are characterized by large heads and elongate bodies that taper to a whip-like tail. They range in size from small, slender-bodied fishes of 1–2 ft in total length (about 30.5–61 cm), to massive fishes, nearly 4 ft in length (122 cm), with gigantic heads and large girth. The skin is smooth and rubbery, completely lacking in scales or denticles. The four gill openings on each side of the head are covered by a fleshy operculum. The mouth is small with teeth that are formed into three pairs of non-replaceable tooth plates, two pairs in the upper jaw and one pair in the lower jaw. These tooth plates tend to protrude from the mouth like a rodent's incisors, suggesting the common names ratfish or rabbitfish for some of the species. The pectoral fins of chimaeras are broad and wing-like and serve to propel the fish through the water by a flapping motion much like underwater flying. All chimaeras have two dorsal fins; the first is preceded by a stout and often toxic spine, and the second is spineless. The lateral line canals are visible externally, and in many species are formed as open grooves. Chimaeras are sexually dimorphic. Adult males possess three unique secondary sexual characteristics: a bulbous, denticulate frontal tenaculum that rests in a pouch atop the head; blade-like prepelvic tenaculae that are hidden in pouches anterior to the pelvic fins; and pelvic claspers that extend from the posterior edge of the pelvic fins.

Distribution

These fishes are entirely marine and are distributed in all of the world's oceans with the exception of Arctic and Antarctic waters. Most species live in deep waters of the shelf and slope, generally at depths greater than 1,500 ft (457 m), and the deepest recorded capture was near 9,000 ft (2,743 m). Although most chimaeras are deepwater dwellers, several species occur in shallower waters, and some migrate inshore. Many species are known from a very widespread geographic range, sometimes throughout an ocean basin spanning the northern and southern hemisphere, while other species appear to be more restricted in their range both vertically and horizontally.

Habitat

Chimaeras usually live on or near muddy bottoms. They tend to remain close to the bottom and are not known to

move into the pelagic zone. Most species occur near continental landmasses or off oceanic islands and on the slopes of seamounts and underwater ridges.

Behavior

Some species are locally migratory and congregate near the shore for breeding and spawning. It also has been observed that some chimaeras tend to aggregate into single-sex groups and to separate into groups based on age.

Feeding ecology and diet

The diet consists primarily of benthic invertebrates. The tooth plates are used to crush hard-bodied prey such as crabs, clams, and echinoderms. Chimaeras also are known to prey upon other fishes. Very little information exists with regard to predation of chimaeriformes; their main predators are sharks and humans.

Reproductive biology

Most species reach sexual maturity at about 18 in (45.7 cm) body length measured from the distal edge of the gill opening to the origin of the dorsal lobe of the caudal fin. Females are generally larger than males. Like their shark relatives, chimaeras have internal fertilization in which males, equipped with pelvic claspers, transfer sperm directly into the female reproductive tract. Males also possess two additional organs used in copulation. Unique to chimaeroids is the club-like frontal tenaculum that emerges from the top of the head in sexually mature males and has been observed to be used to grasp the posterior edge of the pectoral fin of the female during courtship. Additionally, a pair of blade-like prepelvic tenaculae aid in anchoring the male during copulation. Sperm storage in females has been observed in one species and is likely to occur in all species.

All species of chimaeras are oviparous and reproduce by laying eggs. Fertilized eggs are encased in egg capsules and deposited onto the ocean floor. Egg capsules are laid in pairs with each egg capsule containing only a single egg. The egg capsules are generally spindle shaped, sometimes with broad lateral web-like flanges that vary in size and shape depending on the species. Embryological development may take six to twelve months, and fully developed hatchlings measure about 5 in (12.7 cm) in length and look like miniature adults. Very little is known about details of reproduction and development for most species of chimaeras.

Conservation status

There is insufficient data to determine if any species of chimaeras are threatened. However, chimaeras may be inadvertently subject to overexploitation from fisheries due to lack of understanding of their age, growth, and population structure, and seemingly low fecundity.

Significance to humans

A few species of chimaeras are fished commercially for human consumption, particularly in the southern hemisphere; however, most species of chimaeras are little used and are unlikely to become an important fishery resource. Chimaeras are sometimes taken as minor bycatch in trawls and can be processed for oil and fishmeal.

1. Female spotted ratfish (*Hydrolagus colliei*); 2. Female Pacific spookfish (*Rhinochimaera pacifica*); 3. Female ghost shark (*Callorhinchus milii*). (Illustration by Dan Erickson)

Species accounts

Ghost shark
Callorhinchus milii

FAMILY
Callorhinchidae

TAXONOMY
Callorhinchus milii Bory de St. Vincent, 1823, Australia.

OTHER COMMON NAMES
English: Elephant shark, whitefish; Maori: Reperepe.

PHYSICAL CHARACTERISTICS
Distinguished by a plow-shaped snout. Unlike other chimaeras, all of which have whip-like tails, callorhinchids have externally heterocercal tails with a large dorsal lobe and smaller ventral lobe. Body color is silvery and is black along the dorsal midline and top of the head with black saddle-like bands along the dorsal surface of the trunk.

DISTRIBUTION
Southern coasts of New Zealand and Australia.

HABITAT
Prefers coastal waters, living on or near sandy, muddy, or rocky bottoms.

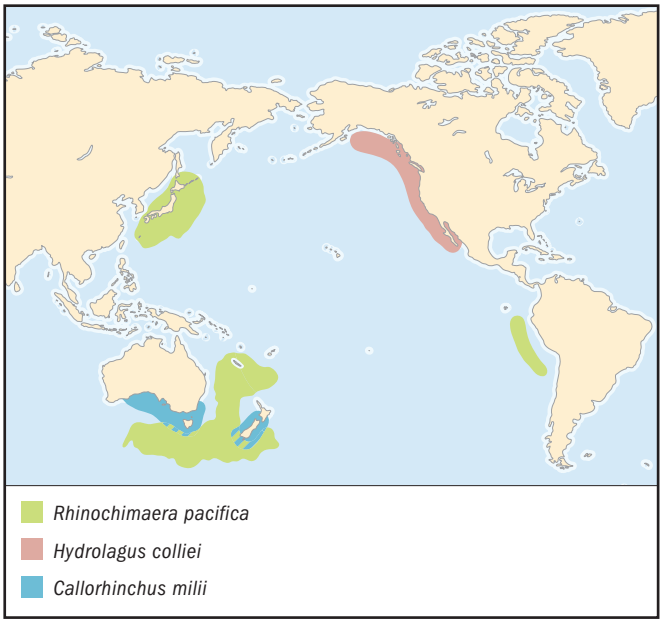
BEHAVIOR
Known for seasonal migration inshore to spawn in shallow coastal waters.

FEEDING ECOLOGY AND DIET
Feeds on benthic invertebrates, particularly small bivalves. It may also eat other fishes.

REPRODUCTIVE BIOLOGY
This is an oviparous species, with eggs fertilized within the female reproductive tract. Females lay two eggs at a time, each contained within its own egg capsule, over a period of months. Development appears to take 6–12 months.

CONSERVATION STATUS
Large fluctuations in population size have been recorded in New Zealand with a general trend toward decreasing numbers over the years. This species may be impacted by overfishing.

SIGNIFICANCE TO HUMANS
Commercially fished and used for human consumption in New Zealand and Australia. ◆



Spotted ratfish
Hydrolagus colliei

FAMILY
Chimaeridae

TAXONOMY
Hydrolagus colliei Lay and Bennett, 1839, Monterey, California.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head contains a bluntly pointed snout. Body color is a reddish to dark brown with silvery-blue and gold highlights, as well as numerous small white spots on the head and along sides and back of the trunk. Ventrally the color is an even pale cream or gray.

DISTRIBUTION
Southeastern Alaska to Baja, California, and the northern Gulf of California. It has been recorded at depths ranging from the surface to 2,995 ft (912.9 m).

HABITAT
Usually occurs near muddy, sandy, or rocky bottoms.

BEHAVIOR
Known to migrate from deeper to shallower waters. It tends to aggregate into groups based on age and sex.

FEEDING ECOLOGY AND DIET
Feeds on benthic invertebrates and other fishes.

REPRODUCTIVE BIOLOGY
Oviparous, with eggs fertilized within the female reproductive tract. Two egg capsules, each containing a single embryo, are laid every 7–10 days for a period of months. Development appears to take 6–12 months.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
At one time this species was fished locally for the oil extracted from the liver. There is no known commercial value, and it is considered a nuisance fish by local fishermen. ◆

Pacific spookfish
Rhinochimaera pacifica

FAMILY
Rhinochimaeridae

TAXONOMY
Rhinochimaera pacifica Mitsukuri, 1898, Japan.

OTHER COMMON NAMES
English: Knifenose chimaera; Spanish: Tucán; Japanese: Tengu-ginzame.

PHYSICAL CHARACTERISTICS
A long, narrow conical snout extends forward from the head. The body is elongate and tapering to a whip-like tail. Body color is usually a uniform brown or grayish brown, with fins a darker shade. The skin along the ventral side of the snout and around the mouth is generally white in color.

DISTRIBUTION
Widely distributed throughout the western Pacific Ocean from Japan to subantarctic waters. Also reported from the southeastern Pacific of Peru.

HABITAT
Inhabits deep water slopes and seamounts usually associated with muddy bottoms.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Diet consists of a wide variety of benthic invertebrates and possibly other fishes.

REPRODUCTIVE BIOLOGY
Oviparous, with eggs fertilized within the female reproductive tract. Females lay two egg capsules at a time, each containing a single embryo. Very few egg capsules and embryos have ever been observed, and almost nothing is known of spawning and embryological development in rhinochimaerids.

CONSERVATION STATUS
Insufficient information is available.

SIGNIFICANCE TO HUMANS
Not known to be commercially fished, although it may be caught as bycatch and processed for oil or fishmeal. ◆

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Dominique A. Didier, PhD

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Heterodontiformes

(Bullhead or horn sharks)

Class Chondrichthyes
Order Heterodontiformes
Number of families 1

Photo: A California bullhead shark (*Heterodontus francisci*) near San Clemente Island, California. (Photo by Animals Animals ©Randy Morse. Reproduced by permission.)

Evolution and systematics

The earliest fossil bullhead (or horn) shark known from articulated specimens is from the marine late Jurassic strata of Solnhofen, southern Germany (about 150 million years old). However, fragmentary remains are known from the early Jurassic of Germany, and most fossil bullhead species have been described from isolated teeth or finspines from Cretaceous and Tertiary deposits of Europe, North and South America, Australia, and Africa. These fossils indicate that bullhead sharks have occupied shallow marine environments throughout their long history.

Bullhead sharks are part of the superorder Galeomorphii, a group that also contains the carpet sharks (Orectolobiformes), mackerel sharks (Lamniformes), and ground sharks (Carcharhiniformes). These orders have the hyomandibular fossa closely adjacent to the orbit on the neurocranium (this fossa, or depression, anchors the hyomandibula, a cartilage that connects distally to the jaw joint, to the skull). Bullhead sharks were believed to be closely related to more primitive Mesozoic hybodont sharks (which also had dorsal finspines), and therefore considered to be living relics, but it is now well established that bullheads share a common ancestry with modern (galeomorph) sharks. However, the phylogenetic relationships among bullhead species have not been satisfactorily studied. All bullhead species are classified in the single family Heterodontidae.

Eight living species of bullheads are currently recognized, all in the single genus *Heterodontus*. Most species have been described in the mid- to late nineteenth century, but *H. portusjacksoni* was described in 1793, and two species have been discovered and named in the twentieth century (in 1949 and 1972). Additionally, there is one undescribed species of bullhead shark off southern Oman, in the northwestern Arabian Sea. Most living species of bullheads have been relatively well characterized, but some species (such as *H. portusjacksoni*) are far better known than others (such as *H. ramalheira*).

Physical characteristics

Bullhead sharks have a tapered profile due to their large, bulky heads. Their snouts are blunt, short, and rounded. Bullheads also have prominent supraorbital ridges (elevated crests supporting the eyes), which provide a greater range of vision, possibly an advantage for bottom-dwelling sharks. Bullheads have two relatively large dorsal fins (the first is clearly larger than the second), each preceded by a short finspine. The finspine in embryos is blunt so as to not harm the mother, but relatively sharp in adults. The caudal fin is robust, with a prominent notch separating the upper and lower lobes. There are five pairs of gill slits. Bullheads are covered with large, abrasive dermal denticles, which are visible without magnification.

Bullheads are the only living sharks with a finspine preceding each dorsal fin in combination with presenting an anal fin. They also have unique dentitions, with small anterior teeth endowed with small cusps for clutching prey, contrasting to the more posterior tooth rows where the teeth are flattened and enlarged (up to 0.4 in/1 cm wide), adapted for grinding hard-shelled invertebrates (hence the generic name *Heterodontus*, meaning "having different teeth"). Their nostrils are also unique, being very large and circular, providing

A Port Jackson shark (*Heterodontus portusjacksoni*) swimming with fish. (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

them with a well-developed sense of smell that is also important for bottom-dwelling species.

Coloration is helpful to distinguish among bullhead species. Three species present light-brown to grayish-brown background coloration with darker-brown spots on the head, body, fins, and tail (*H. francisci*, *H. quoyi*, and *H. mexicanus*) but the arrangement, number, and diameter of the spots is usually distinct for these species. *Heterodontus ramalheira* is unique in having a reddish-brown background with creamy-white, minute spots. *Heterodontus japonicus* and *H. galeatus* have dark saddlelike markings on their dorsal surfaces (and also over the eyes and underneath the first dorsal fin in the latter species), both with lighter background colors. *Heterodontus portusjacksoni* is unique in the genus in presenting a horizontal pattern of brownish-black stripes. However, the most spectacular of all bullhead species, and one of the most ornate sharks known, is *H. zebra*, with an intense, dark brownish-black vertical-stripe pattern from head to tail and over the pectoral fins, with some of the stripes coupled together along the sides of the trunk.

Bullheads are only average-sized sharks, reaching from 28–51 in (70–130 cm) long, but a few species may reach slightly larger sizes. Most species are sexually mature when between 15.7–28 in (40–70 cm) long for males, and slightly larger for females.

Distribution

Three species are present in the tropical eastern Pacific: *H. francisci*; *H. mexicanus*, distributed in the Gulf of California, along the Central American coast down to Colombia and possibly Peru; and *H. quoyi*, found in the Galápagos Islands and the coasts of Ecuador and Peru. Two species are Australian: *H. galeatus* (eastern Australia and perhaps in Tasmania and off Cape York) and *H. portusjacksoni* (southern [including Tasmania], western, and eastern Australia, and possibly in New Zealand). *Heterodontus ramalheira* occurs along the eastern African coast extending northward to the Arabian Peninsula; *H. japonicus* is a western Pacific species, occurring around Japan, Korea, and off the Chinese coast; *H. zebra* is somewhat widespread in the western Pacific, distributed from Japan and Korea down to Vietnam, with records also in Indonesia and northwestern Australia.

Habitat

Bullheads inhabit the continental shelf, usually in shallow waters from the intertidal zone down to about 328 ft (100 m), and less frequently at greater depths (to 820 ft/250 m for *H. ramalheira* and *H. portusjacksoni*). They occur on hard and soft bottoms, including reefs, rocky, and sandy substrates, and commonly frequent caves, crevices, and kelp and sea grass beds.

Behavior

Bullheads are more active nocturnally, as are many benthic sharks. They are usually solitary, although recently born individuals may group together for a small period before going their separate ways, and aggregations of adults have been observed in some species. Their strong pectoral fins are used to "walk" over the substrate. In the most-studied species, (*H. portusjacksoni*), adults tend to occupy a restricted range, returning to the same resting location daily, and there is a certain degree of territoriality and competition for favored resting caves. Courtship patterns have been observed in *H. francisci.* At least one species, *H. portusjacksoni*, appears to be migratory, returning to breeding sites after periods spent in deeper waters.

Feeding ecology and diet

Bullheads consume abundant amounts of hard-shelled benthic invertebrates, including crabs, lobsters, shrimp, barnacles, starfish, urchins, gastropods, and polychaetes. Most species also eat fishes. Smaller individuals eat softer prey items while their molariform posterior teeth are still in development. Bullhead sharks commonly employ strong suction feeding. One bullhead shark has been found in the stomach of a tiger shark, but they are generally avoided as prey because of their finspines.

Reproductive biology

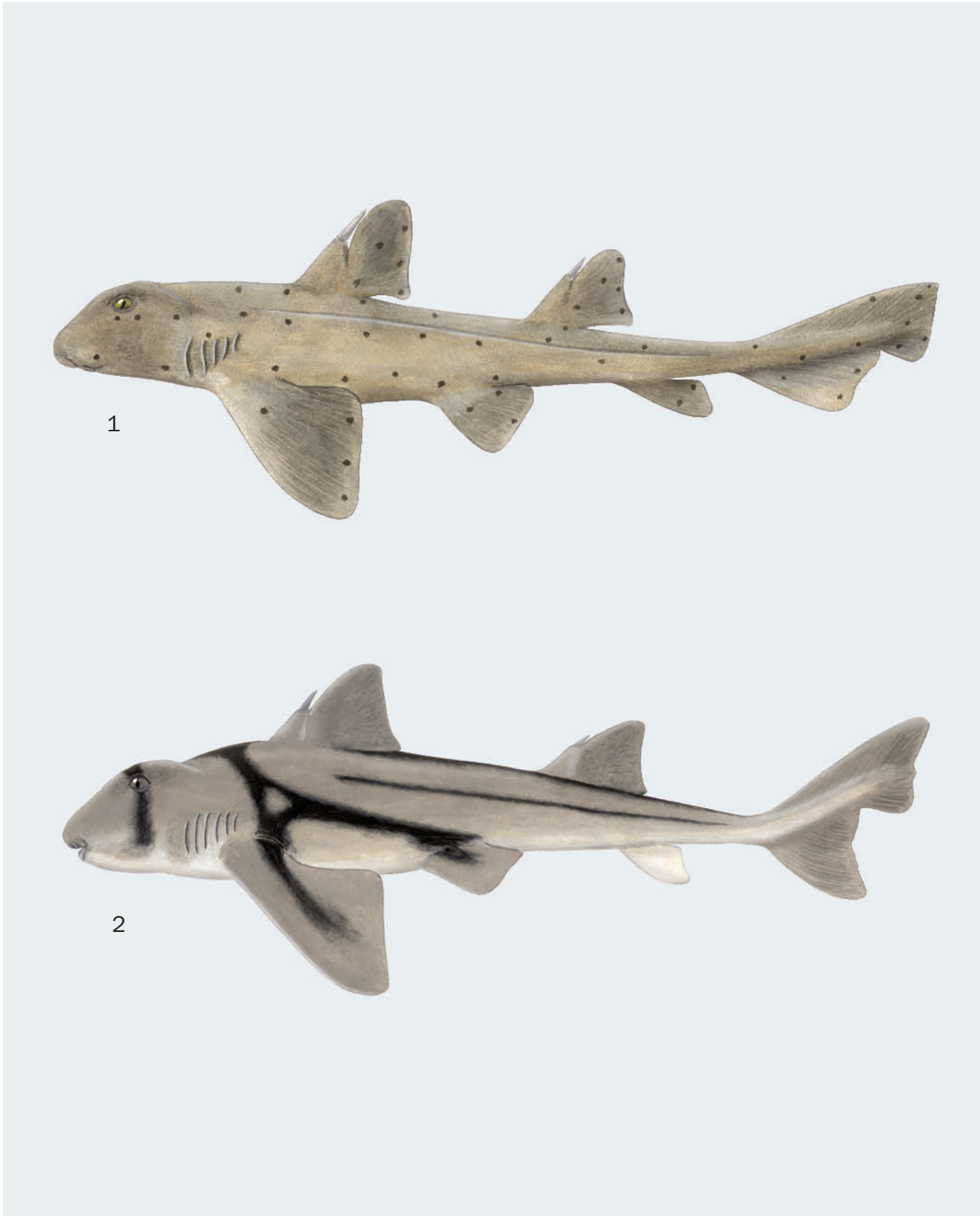
All bullhead sharks have internal fertilization and are oviparous (egg-laying), laying large, spiral-rimmed egg cases. The fully formed egg cases are expelled rather early by females, so that most fetal development occurs in the egg cases while in the environment, not inside the mother. Young hatch from between five and 12 months after being laid, one per egg case, and measure about 3.9–5.5 in (10–14 cm). The young often move into nursery areas or bays after hatching. The egg cases are laid in shallow water, sometimes in unguarded "nests" (*H. japonicus*), and usually in protected kelp beds or enclosed in protected areas (the egg may be carried and lodged by the mother, using her mouth, in a crevice). Adults have been observed to eat their own egg cases.

Conservation status

Not threatened.

Significance to humans

Their significance is mostly recreational (e.g., when observed by divers), as bullheads are not consumed on a regular basis. They are caught as bycatch in bottom trawls and usually discarded, but they may be occasionally consumed or used as fishmeal (off eastern Mexico, for example). Various species of bullheads are commonly kept in public and private aquaria, where they can be maintained successfully for over a decade.



1. California bullhead shark (*Heterodontus francisci*); 2. Port Jackson shark (*Heterodontus portusjacksoni*). (Illustration by Dan Erickson)

Species accounts

California bullhead shark
Heterodontus francisci

FAMILY
Heterodontidae

TAXONOMY
Cestracion francisci Girard, 1854, California (Monterey Bay).

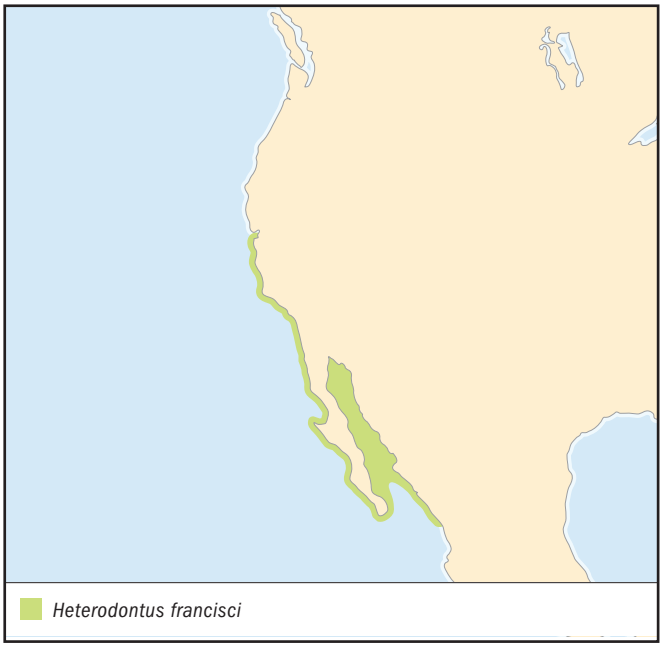
OTHER COMMON NAMES
English: Bullhead shark, horn shark; Spanish: Dormilón cornudo.

PHYSICAL CHARACTERISTICS
Background gray or light brown with smaller darker brown spots (smaller than eyes) scattered over body, head, fins, and tail. The young have more intense coloration, sometimes with darker bands in between eyes and on fins. The supraorbital ridges are moderately high; finspines relatively tall, but dorsal fins are not as tall as in *H. zebra* and *H. japonicus*.

DISTRIBUTION
California bullhead sharks occur off central and southern California and Mexico (Baja California and Gulf of California), extending south possibly to Ecuador and Peru. During warm water influxes, they may reach as far north as San Francisco Bay.

HABITAT
These sharks commonly inhabit from 6.6 to 33 ft (2–10 m), even though they can be found from the intertidal zone down to about 490 ft (150 m). Juveniles are usually in shallower waters, over sandy surfaces. These fishes occur on rocky and sandy bottoms, kelp forests, and in caves and crevices.

BEHAVIOR
These sharks are nocturnal, sluggish, and mostly solitary, preferring the protection of caves and shelters during the day, and hunting mostly at night. They can remain in a relatively small home range for much of the summer, moving into deeper waters in the winter, at least in some regions. Experiments demonstrate that their diel (24 hours, including one day and night) activity patterns appear to be regulated by light.



FEEDING ECOLOGY AND DIET
California bullhead sharks eat many different invertebrates, including sea urchins, crabs, shrimp, isopods, octopuses, anemones, bivalves, gastropods, polychaetes, and occasionally fishes (at least pipefishes [Syngnathidae] and blacksmiths [Pomacentridae]). Specimens have been filmed devouring purple-colored urchins, turning their teeth and spines into a strong shade of purple. Recently born pups take about one month to begin feeding. Adults in aquaria have been observed consuming their own egg cases.

REPRODUCTIVE BIOLOGY
The mating ritual of California bullhead sharks has been observed in captivity, particularly at the Steinhart Aquarium in San Francisco. Males pursue larger females until obtaining consent, and mating occurs on the bottom of the tank. The male grasps the female's pectoral fin with his teeth, and subsequently one clasper is inserted into the female after coiling around her. Copulation may last between 30 to 40 minutes, and in captivity the eggs are expelled one or two weeks later. In the wild, eggs can be expelled even after one to three months of copulation, as females can produce eggs for extended periods, and sperm is stored and utilized in stages. The young develop for between seven and nine months before hatching.

CONSERVATION STATUS
A decrease in numbers of individuals has been noticed in regions of southern California where there is substantial diving activity, but the species is not listed by the IUCN as Threatened.

SIGNIFICANCE TO HUMANS
These sharks are very common in public aquaria, where mating, egg-laying, and hatching have been observed. In the wild, they are not considered a threat to humans. However, despite their apparent calm demeanor, *H. francisci* have been known to infrequently swim after and bite divers after being harassed by them. ◆

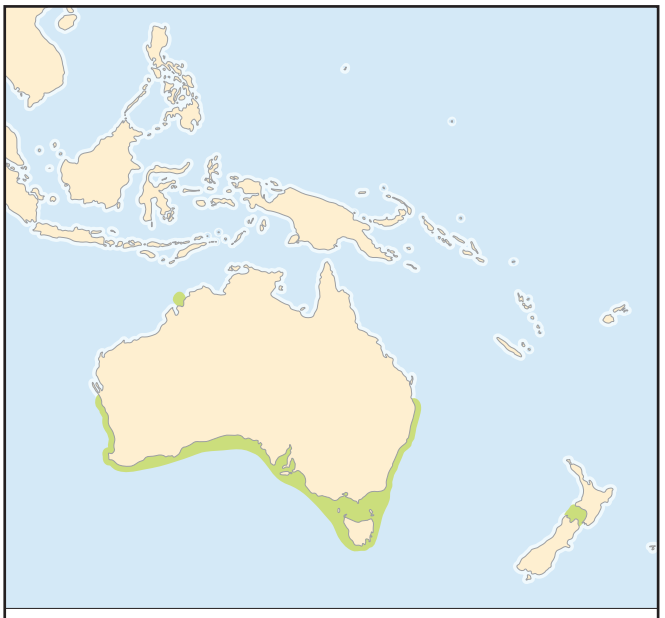
Port Jackson shark
Heterodontus portusjacksoni

FAMILY
Heterodontidae

TAXONOMY
Squalus portus jacksoni Meyer, 1793, Australia (Botany Bay, New South Wales).

OTHER COMMON NAMES
English: Bullhead shark, oyster crusher, tabbigaw.

PHYSICAL CHARACTERISTICS
Port Jackson sharks are distinguished by a gray to brownish background with a harnesslike pattern of darker brown stripes over the pectoral fins and below the first dorsal fin, with a dark stripe across the head and eyes and a few dark oblique stripes



along the trunk. The supraorbital ridges are only moderately high. The finspines do not reach the dorsal fin tips, being rather blunt and short; and the dorsal fins are not nearly as high as in *H. zebra* and *H. japonicus*.

DISTRIBUTION

These sharks occur around the southern, western, and eastern Australian coast, including Tasmania. A single record exists for New Zealand, but this is possibly a stray.

HABITAT

Port Jackson sharks are common on the temperate Australian continental shelf and upper slope, from close inshore down to 902 ft (275 m).

BEHAVIOR

Port Jackson sharks are nocturnal, occurring in caves and shelters during the day, and hunting at night. Seasonal migrations are frequent, and these may extend 528.2 mi (850 km) in one direction, after which they may return to the same localities each year. Migrations from Sydney to Tasmania have been reported. Captive juvenile Port Jackson sharks may grow 2–2.4 in (5–6 cm) per year; adults grow slightly less at 0.8–1.6 in (2–4 cm) per year. They take in water for respiration through the first gill slit while feeding, freeing their mouths for eating, as water exits from the remaining gill slits.

FEEDING ECOLOGY AND DIET

These sharks primarily eat benthic invertebrates, especially echinoderms, but prey items include crabs, shrimp, starfish, bivalves, gastropods, polychaetes, and small fishes.

REPRODUCTIVE BIOLOGY

These sharks segregate by size after hatching, but adults have been reported to segregate by sex. Adult males move into deeper water toward the end of the breeding season in winter, and adult females migrate shortly thereafter. Females lay from 10 to 16 egg cases in rocky substrates, in sheltered, shallow areas (ranging from 4 to 98 ft [1–30 m], but more commonly from 4 to 16 ft [1–5 m]). Females may utilize the same nesting sites repeatedly, and some have been observed to purposely wedge their egg cases into crevices. Adults may eat their egg cases. The young hatch after nine to twelve months, and quickly move into nursery areas. Maturity ages vary from eight to ten years for males and from eleven to fourteen years for females.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Port Jackson sharks are taken as bycatch in benthic or demersal fisheries, but are not generally consumed. They are very common in public aquaria. The Port Jackson shark is perhaps the best known of all bullhead species, and is not dangerous to humans, although caution is necessary when approaching them. ◆

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Marcelo Carvalho, PhD

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Orectolobiformes
(Carpet sharks)

Class Chondrichthyes
Order Orectolobiformes
Number of families 7

Photo: Banded cat sharks (*Chiloscyliium punctatum*) live around coral reefs and tidepools. This is a juvenile cat shark. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The exact origin of this group is unclear. The Orectobiformes have a Jurassic record and show relationships to the Hybodontiformes, Squatiniformes, and Squaliformes, with such common characters as a flange on the teeth and nasal barbels.

The order Orectolobiformes comprises seven families: the Rhincodontidae (whale shark), the Stegostomatidae (zebra shark), the Orectolobidae (the wobbegongs), the Ginglymostomatidae (the nurse sharks), the Parascyllidae (the collared carpet sharks), the Brachaeluridae (the blind sharks), and the Hemiscyllidae (the longtail carpet sharks).

Physical characteristics

The Orectolobiformes are small to very large sharks with prominent nasoral grooves (grooves connecting the nostrils to the mouth), nasal barbels, two dorsal fins, an anal fin, and small terminal or subterminal mouths.

Distribution

The Orectolobiformes are mainly an Indo-Pacific species. Only two species are found in other oceans. The nurse shark (*Ginglymostoma cirratum*) is found in both the Pacific and Atlantic Oceans. The whale shark has worldwide distribution.

Habitat

With a few exceptions, most of the species of the order are found in the shallow waters of the continental shelves. They often are bottom dwellers in rocky areas or coral reefs. The whale shark is the only pelagic species in the order.

Behavior

Most orectolobiformes are sluggish bottom-dwelling sharks that hide among the bottom rocks or coral heads during the day. Almost nothing is known about the behavior of most species.

Feeding ecology and diet

Most of the orectolobiformes are small, sluggish sharks that feed on small invertebrates and fishes. The whale shark, the largest fish in the world, with a maximum length of 39 ft (12 m), feeds on plankton. Little information exists on creatures that are predatory towards fishes in this order, but carcharhinid sharks are known to prey on small orectolobiformes.

Reproductive biology

Both oviparous and viviparous species have been reported. Little is known about the reproductive processes of most orectolobiformes. The reproductive processes of the nurse shark are probably the best known (see species account following).

Conservation status

Most species in the order are not threatened by fisheries. Recently, there have been localized fisheries for whale sharks in the Philippines, India, and Taiwan. There are no fisheries for them in the Atlantic. The whale shark has been protected in several countries, primarily on aesthetic grounds. Two species are listed on the IUCN Red List: the blue-gray carpet shark (*Heteroscyllium colcloughi*) and the whale shark (*Rhincodon typus*). Both are categorized as Vulnerable. In addition, the whale shark was added to CITES Appendix II in December 2002.

Significance to humans

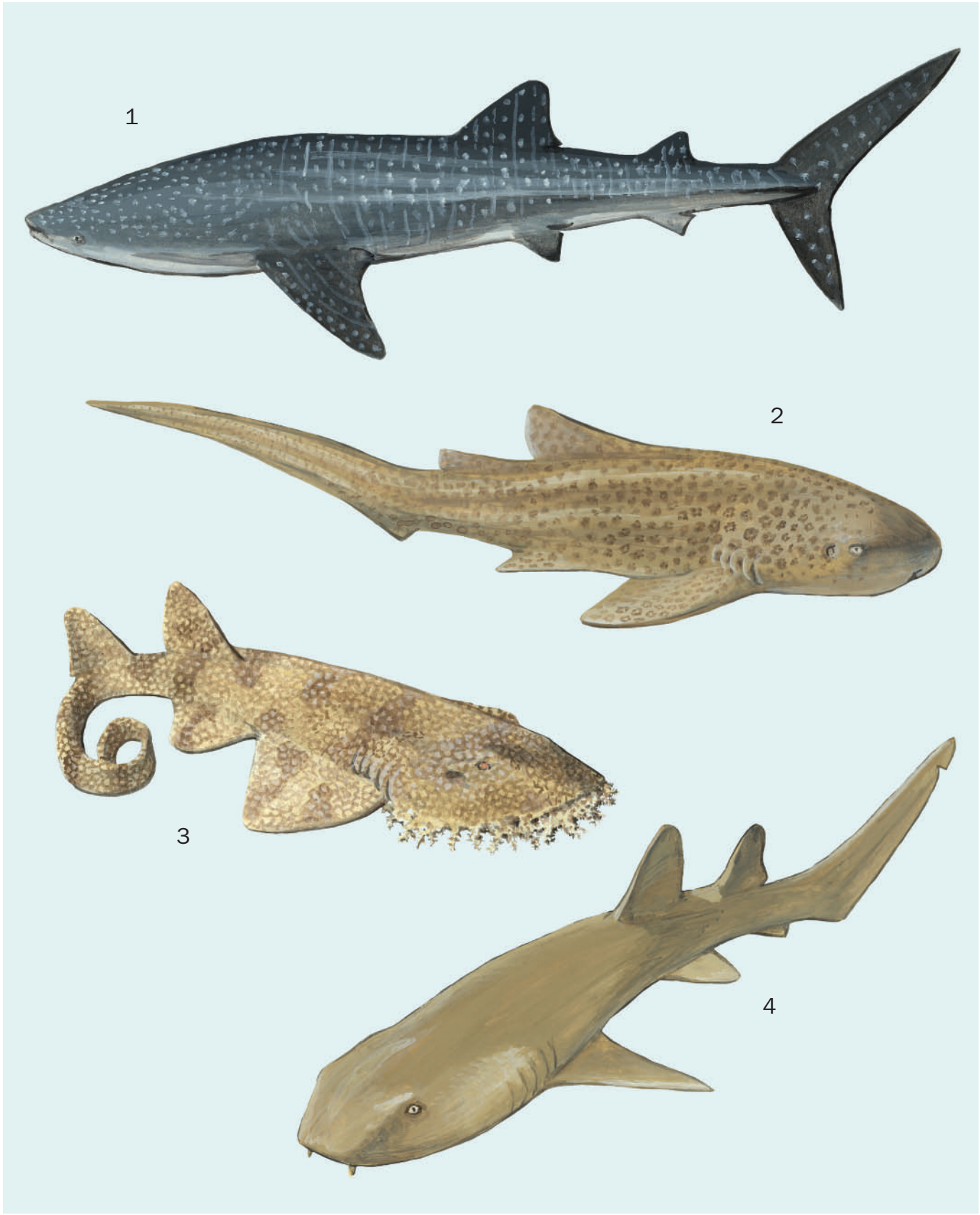
Most Orectolobiformes have little, if any, commercial importance. Some species are found in the aquarium trade. The nurse shark has been used for its liver oil, hides, and meat. Nurse shark liver oil was used for various purposes in the past. In Jamaica, the nurse shark was fished solely for its liver, which was used in burning; a fish yielded about a gallon of

A carpet shark (*Orectolobus maculatus*) yawning. (Photo by Tom McHugh/ Photo Researchers, Inc. Reproduced by permission.)

oil. In the Florida sponge fisheries of the 1880s, fishermen used nurse shark liver oil to calm the water surface so that they could scan the bottom continuously. A teaspoon of oil was said to produce a smooth surface for as long as a small boat of fishermen worked in one spot. People in Key West killed nurse sharks in summer and extracted the oil, which, at the time, sold for one dollar per gallon.

The hides of the nurse shark were the most valuables hides in the Florida shark fishery of the 1940s. Nurse shark hides were bought by the shark leather industry at prices about 25% higher than those of other species. The price of a 90-in (230 cm) hide was about $3.10 in 1943. At present, nurse sharks are little utilized in Florida. Some nurse sharks are fished for crab bait. The fins are worthless in today's industries.

Although the nurse shark is edible, its meat is very seldom found in Florida markets at this time. This limited utilization affords little protection to the species—many shark fishermen kill nurse sharks caught in their longlines, because they consider them a nuisance species that takes baits intended for other species. The species is included in the Fishery Management Plan for Sharks of the Atlantic Ocean, which has regulated the shark fisheries of the East Coast of the United States since 1993. The ability of the nurse shark to survive in confinement and its hardiness have made it the most popular aquarium and laboratory shark. It is certainly the most commonly displayed shark in aquaria throughout the Americas.



1. Whale shark (*Rhincodon typus*); 2. Zebra shark (*Stegostoma fasciatum*); 3. Tasseled wobbegong (*Eucrossorhinus dasypogon*); 4. Nurse shark (*Ginglymostoma cirratum*). (Illustration by Brian Cressman)

Species accounts

Nurse shark
Ginglymostoma cirratum

FAMILY
Ginglymostomatidae

TAXONOMY
Ginglymostoma cirratum Bonaterre, 1788, type locality not specified.

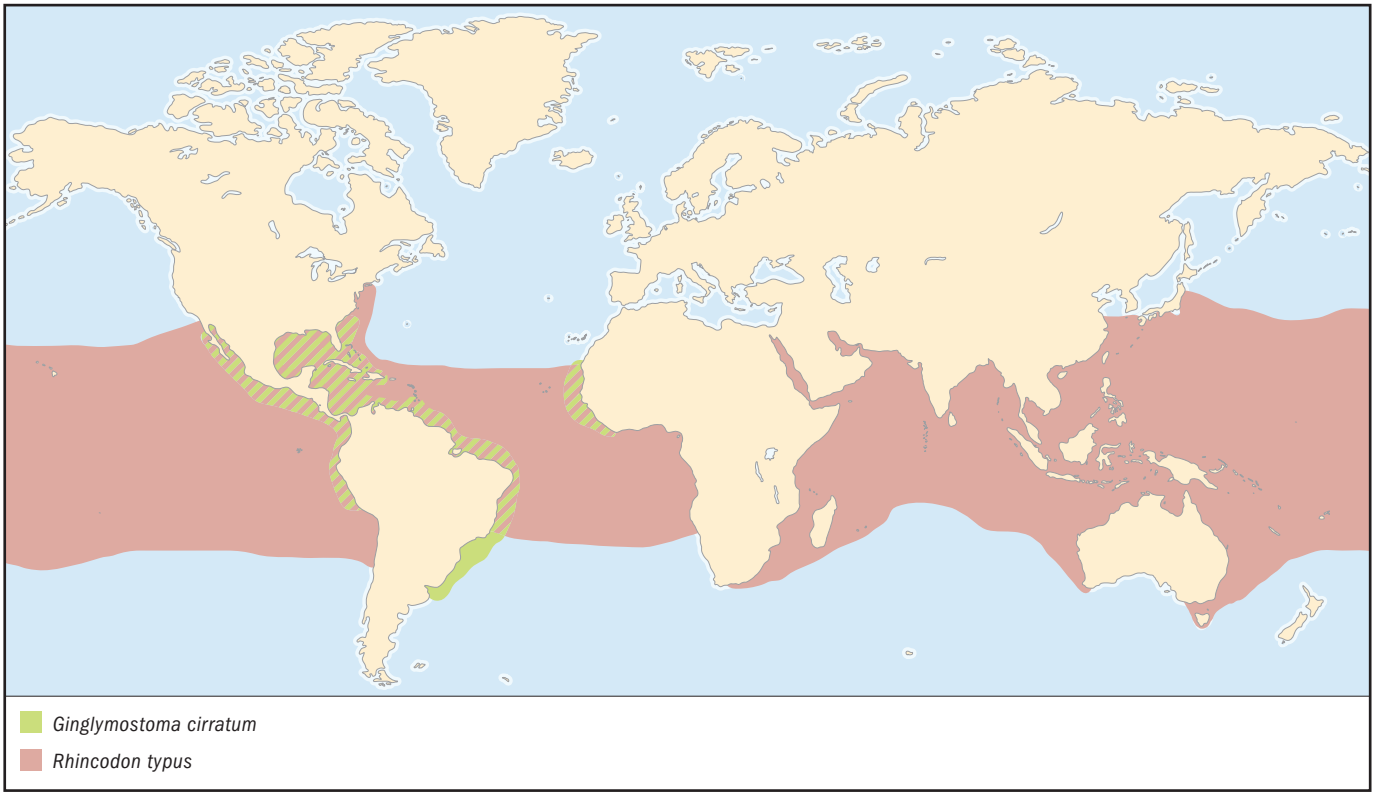
OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Recognized by its conspicuous, long nasal barbels on the anterior margins of the nostrils and first dorsal fin originating over or posterior to the pelvic fin origin. Very wide head that gives it a tadpole appearance from above. Mouth is full of minute teeth, which are similar in both jaws. Teeth have one large cusp flanked on each side by two or three cusplets. Coloration ranges from rich yellowish to grayish-brown, with most specimens being reddish-brown. Yellow and even white specimens have been reported. Newborn nurse sharks have small black spots over the entire body, with an area of lighter pigmentation surrounding each spot and with bands of lighter and darker pigmentation alternating along the dorsal surfaces. The spots disappear by the time the specimens reach 20 in (50 cm) in length. Capable of limited color changes according to light intensity. Although the size and weight attained by the nurse shark often have been exaggerated in both the scientific and popular literatures, no specimen measured by researchers has exceeded 110 in (280 cm) in length. The largest specimen measured and weighed by Castro in Florida was 106 in (268 cm) long and weighed 243 lb (110 kg). The sizes of 132–144 in (335–365 cm) found in the literature must be considered exaggerations caused by Fowler's inaccurate estimates.

DISTRIBUTION
Distributed widely in littoral waters on both sides of the tropical and subtropical Atlantic. Ranges from tropical West Africa to the Cape Verde islands in the east and from southern Brazil to North Carolina and Rhode Island in the west. Also found on the western coast of America from the Gulf of California to Panama and Ecuador. Abundant in the shallow waters of tropical Florida and the Caribbean.

HABITAT
Small juveniles are found in shallow coral reefs and grass flats. Juveniles ranging in size from 47 to 67 in (1,200–1,700 mm) are found around shallow reefs and mangrove islands. Larger juveniles and adults are found near reefs and rocky areas at depths of 66–75 ft (20–75 m) during the daytime and in much shallower areas at night.

BEHAVIOR
Can be found resting on the bottom in small groups during the daytime, concealed under ledges or among boulders and rocks. These sharks often are in very close proximity to and



sometimes almost on top of one another. At dusk they disperse to search for food.

FEEDING ECOLOGY AND DIET
Said to feed chiefly on invertebrates (squids, shrimps, crabs, spiny lobsters, and sea urchins) and small fishes. A recent study of Florida nurse sharks showed that it is an opportunistic predator that consumes a wide range of species of small bony fishes, 3–9 in (8–23 cm) in length, primarily grunts. Prey typically is captured through a powerful sucking action. This suction accounts for the coral debris and solitary corals occasionally encountered in the stomach contents. Castro's study did not support the common belief that the nurse shark preys heavily on spiny lobsters and other crustaceans.

REPRODUCTIVE BIOLOGY
The nurse shark is a viviparous species without a placenta. In Florida and the Bahamas the mating period apparently extends from the last week in May to July, but most observations of mating have been made in mid-June. The embryos are enclosed in horny egg capsules for the first weeks of gestation. Embryos hatch out of the egg cases when they reach 8.9–9.2 in (21.8–23.3 cm). The embryos are lecithotrophic, that is they are fed from yolk stored in a yolk sac, and there is no evidence of any other mode of embryonic nourishment.

The embryos are in different developmental stages through the first four months of gestation. In females examined in October, some embryos measuring 8.5–9.2 in (21.5–23.3 cm) were still inside the egg cases, while others measuring 10.6–10.9 in (27–27.8 cm) had fully absorbed yolk sacs, open yolk sac scars and appeared ready for birth. During the last month of gestation all the embryos were in the same stage of development, that is, they all had absorbed the yolk sac and apparently were ready for birth. These embryos at different stages may have been a result of ovulation of the very large oocytes (2.3–2.4 in, or 5.9–6 cm, in diameter) and encapsulation of the eggs, lasting for two or three weeks, and of the very rapid development of the embryo thereafter. Females expel the empty egg cases after the embryos have hatched out of them.

The embryos measure 11.4–12 in (29–30.5 cm) at birth, after a gestation period estimated at about five to six months. Brood sizes are large, ranging from 21 to 50 young, with a median of 32. Aquarium observations on parturition suggest that the young are released over a period of a few days, usually at night. The reproductive cycle of the nurse shark encompasses a five- to six-month gestation period and a biennial reproductive cycle. After the gestation period of five to six months and birth in late November or early December, a female does not mate again until 18 months later, in June; thus reproduction is biennial.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The greatest value of the nurse shark probably lies in ecotourism. The nurse shark is the species of shark most often seen by recreational divers in Florida and the Caribbean. Because it is a large but harmless species, the nurse shark thrills divers that see one unexpectedly or at close range. In the last decade, numerous shark-watching operations have emerged in Florida and the Bahamas. In some locations nurse sharks have become habituated to being fed by divers. Although the long-term consequences and risks of these operations are still unclear, one can hope that public awareness and concern may result in some form of protection for these interesting animals. This species is one of the most common sharks in aquaria, because of its hardiness and its ability to survive in confinement for many years. According to Clark, one specimen survived 25 years at the Shedd Aquarium in Chicago, and another lived for 24 years at the Government Aquarium in Bermuda. The nurse shark is one of the most important species in shark research. ◆

Tasseled wobbegong
Eucrossorhinus dasypogon

FAMILY
Orectolobidae

TAXONOMY
Eucrossorhinus dasypogon Bleeker, 1867, Indonesia.

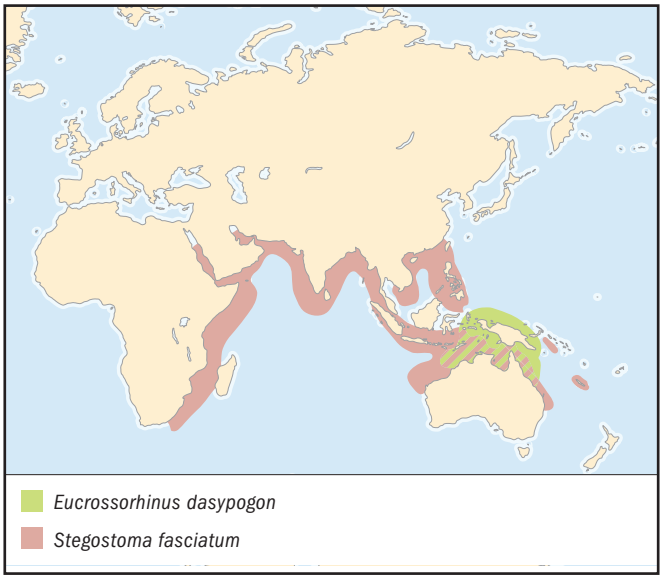
OTHER COMMON NAMES
English: Ogilby's wobbegong.

PHYSICAL CHARACTERISTICS
Bottom-dwelling, large shark with flattened body, wide mouth, and two dorsal fins set far back in the body. Head very flat, with a frill, or beard, of fleshy protuberances, known as dermal lobes, surrounding the outline of the head. These protuberances serve to break up the outline of the head against the bottom vegetation or rocks. Color is yellowish-brown or grayish-brown, with numerous reticulations and blotches. Coloration and frill of dermal lobes surrounding the outline of the head camouflage the shark very effectively against the bottom.

DISTRIBUTION
Western South Pacific in the shallow waters of Indonesia, Papua New Guinea, and northern Australia.

HABITAT
Found in shallow coral reefs. Poorly understood but the most commonly observed wobbegong in the Great Barrier Reef.

BEHAVIOR
Appears to be an ambush predator that waits for its prey while camouflaged against the bottom.



FEEDING ECOLOGY AND DIET
Details of its feeding ecology are not known.

REPRODUCTIVE BIOLOGY
Its reproductive processes are not known. It is believed to be ovoviviparous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The species has little economic importance, other than as an attraction for fish watchers. Some attacks on divers have been attributed to this species. Its effective camouflage and large size make it potentially dangerous to divers, who may inadvertently approach it too closely, causing it to bite in self-defense. ◆

Whale shark
Rhincodon typus

FAMILY
Rhincodontidae

TAXONOMY
Rhincodon typus Smith, 1828, South Africa.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Largest fish in the world. The average size for this species is 18–32.8 ft (5.5–10 m). The largest specimen measured was slightly over 39.4 ft (12 m) in length. It is said to grow larger, but no one has actually measured a whale shark over 40.03 ft (12.2 m). Very short snout, with a huge terminal mouth; its nostrils have short, blunt nasal barbels. Three pronounced longitudinal ridges along each side of the trunk, the lowermost ridges becoming strong caudal keels near the tail. Covered with white or yellowish dots and irregular bars. The spots, vertical bars, and longitudinal ridges along the flanks create a checkerboard appearance.

DISTRIBUTION
Cosmopolitan in tropical and subtropical waters.

HABITAT
Pelagic species that often approaches coastal areas.

BEHAVIOR
A sluggish shark, it often is seen swimming slowly on the surface, scooping up plankton and small fishes with its huge mouth.

FEEDING ECOLOGY AND DIET
Feeds on plankton. Plankton feeding is the most common and efficient feeding strategy of the largest sharks and most whales. Despite its being a ubiquitous species, we know very little about its feeding ecology.

REPRODUCTIVE BIOLOGY
This species is viviparous. Very little is known about reproduction of the whale shark, because only one gravid female has been examined. On 15 July 1995, a pregnant female was harpooned off the east coast of Taiwan. This female, estimated at about 35 ft (10.6 m) and weighing 17.6 tons (16 metric tons), contained about 300 embryos in the uterui. As in the nurse shark, the embryos were in different stages of development. Some 237 of the embryos measured from 16.5 to 25.2 in (42–64 cm) in length; the largest embryos, at 22.8–25.2 in (58–64 cm), were probably ready to be born. This mode of reproduction is very similar to that of the nurse shark, where lecithotrophic embryos are found at different stages of development and hatch out of their egg cases at different times. This brood of 300 young is by far the largest reported for any elasmobranch.

CONSERVATION STATUS
The whale shark has been the subject of much attention; it is protected in some countries, although there are few actual threats to this ubiquitous species. The only active fisheries at the time of this writing are in India and Taiwan. The effects of these fisheries on the Pacific Ocean population are unknown. There are no whale shark fisheries in the Atlantic Ocean. This species is listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Seeing this gigantic, harmless creature in the water is often an unforgettable experience. One ecotourism operation has developed around Ningaloo Reef, Australia, where whale sharks can be spotted at certain times of the year. Similar operations may develop elsewhere, given the general interest in whale sharks. ◆

Zebra shark
Stegostoma fasciatum

FAMILY
Stegostomatidae

TAXONOMY
Stegostoma fasciatum Smith, 1828, type locality not specified.

OTHER COMMON NAMES
English: Leopard shark.

PHYSICAL CHARACTERISTICS
Large species, reaching more than 9.8 ft (3 m) in length. Stout body with very long tail, almost as long as the rest of the body; short nasal barbels; and spectacular yellow coloration. The young are blackish-brown with vertical yellowish stripes and spots, hence the name zebra shark (although the coloration is the reverse of that of a zebra). Adults are yellowish with dark spots; hence the name leopard shark. Both juveniles and adults are easy to identify.

DISTRIBUTION
Found throughout the Indo-Pacific region.

HABITAT
Shallow coastal areas and coral reefs.

BEHAVIOR
Its behavior is poorly known, except that it often is seen resting on the bottom in coral reef areas.

FEEDING ECOLOGY AND DIET
Feeds primarily on gastropods, bivalves, and small fishes. Consumes large numbers of snails. Their spiral valve intestines often are full of the opercula (the horny or shell covering on a

snail's shell that closes the shell opening) of snails that they have digested, with the opercula stacking up like coins in the intestine.

REPRODUCTIVE BIOLOGY
Oviparous (egg layer). The egg cases are large, about 5.9–3.9 in (15–10 cm), and are provided with hairlike fibers that anchor them to the bottom.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Caught for food throughout its range. Small numbers are captured for the aquarium trade. The large adults are beautiful display fishes in large oceanaria. The species is of little economic importance.

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José I. Castro, PhD

Carcharhiniformes
(Ground sharks)

Class Chondrichthyes
Order Carcharhiniformes
Number of families 8

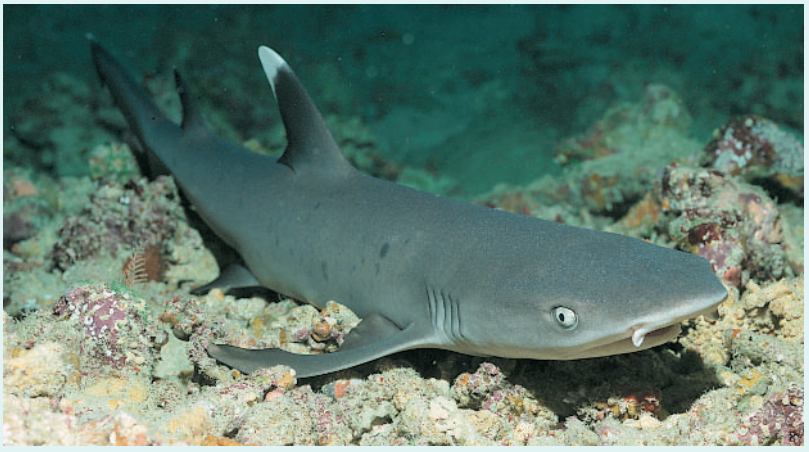


Photo: A whitetip reef shark (*Triaenodon obesus*) resting on coral rubble near Fiji. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The fossil history of ground sharks (Carcharhiniformes) is known from a handful of preserved skeletons, but long intervening periods exist in which fossil skeletons of ground sharks have not been recovered. Ground sharks first appear in the late Jurassic (some 150 million years ago) Solnhofen limestones of Germany. These early fossils (e.g., *Macrourogaleus*) are not well preserved, but they bear some resemblance to modern catsharks (family Scyliorhinidae). After a long absence from the fossil record, fossil ground shark skeletons reappear in the late Cretaceous chalk deposits of Lebanon (ranging in age from 84 to 95 million years ago, or mya). These sharks (e.g., *Pteroscyllium* and *Paratriakis*) are thought to be related to catsharks and hound sharks (Triakidae), respectively, but on scant evidence. A few species of fossil catsharks from Lebanon are even placed in the living genus *Scyliorhinus*, which would give it a remarkable longevity of some 90 million years. These fossils have been studied only superficially, however, and they probably represent extinct genera of uncertain affinity. Partial skeletons are present in the Monte Bolca beds of northeastern Italy (*Eogaleus* and *Galeorhinus*) of Eocene age (some 52 mya), again after a hiatus of more than 30 million years.

Many extinct species of ground sharks are known from isolated teeth, which are widespread and provide a fairly robust stratigraphic record. Tertiary ground shark fossils are relatively modern in their level of diversity. Ground shark fossils are present on every continent, indicating that they have been distributed widely for the past 65 million years at least. Remarkably, the fossil record of ground sharks parallels their phylogenetic history, where the most "primitive" family (Scyliorhinidae) also is the oldest.

Ground sharks are related closely to bullhead (Heterodontiformes), carpet (Orectolobiformes), and mackerel (Lamniformes) sharks among living elasmobranchs (sharks and rays), forming the larger group known as the Galeomorphii. Galeomorph sharks are characterized by several evolutionary innovations, such as the unique placement of the hyomandibula (a cartilage supporting the jaws posteriorly) on the skull. Within the Galeomorphii, carcharhiniforms are related most closely to the mackerel sharks, as they share a tripodal rostrum (the anterior extension of the skull) supporting the snout internally. All carcharhiniforms have specialized secondary lower eyelids ("nictitating" eyelids, which are absent from all other sharks) as well as unique clasper skeletons. Similarly to lamnoids (a subgroup within mackerel sharks), there is also a group of "higher carcharhiniforms" characterized by plesodic pectoral fins (with internal supports reaching the fin margin).

There are approximately 216 species, 48 genera, and eight families in the Carcharhiniformes. This amounts to slightly more than half of all shark species and about half of all shark genera. The eight families are the Scyliorhinidae (catsharks, 15 genera and some 105 species—the largest shark family of any order), Proscylliidae (finback catsharks, three genera and five species), Pseudotriakidae (false catshark, monotypic), Leptochariidae (barbeled hound shark, monotypic), Triakidae (hound sharks, 10 genera and 39 species), Hemigaleidae (weasel sharks, four genera and seven species), Carcharhinidae (requiem sharks, 12 genera and 50 species), and Sphyrnidae (hammerhead sharks, two genera and eight species). New carcharhiniform species have been described in recent years, particularly of catsharks, and additional new species await formal description. Phylogenetic relationships among ground shark genera require further study, which may result in the merging of several currently monotypic genera and even of some of the families.

Physical characteristics

There are many different morphological and ecological trends within the Carcharhiniformes, which is to be expected from a large group that inhabits waters from the intertidal

A tiger shark (*Galeocerdo cuvier*) demonstrating aggressive behavior. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

zone to the lower reaches of the continental slope. However, the morphological differences among ground shark families are not as great compared with the other orders of sharks, even though some families are quite distinctive. One of these families is the hammerhead shark (Sphyrnidae), which is unique among all sharks in having a laterally expanded head (the hammerhead, or cephalofoil, with eyes on the lateral extremes). Hammerhead sharks are otherwise very similar to requiem (carcharhinid) sharks. Catsharks (Scyliorhinidae) also are recognized easily, as their first dorsal fins are situated either on the same level as or behind the pelvic fins. The false catshark (Pseudotriakidae) is unique among sharks in having a first dorsal fin that is much longer than the caudal fin. The differences among the remaining families are subtle, and one must look at their teeth, labial furrows, and even intestines to identify them.

Carcharhiniforms are small, medium, or large sharks; adults usually range from 18 in (45 cm) to 20 ft (6 m) in length. The proscylliid *Eridacnis radcliffei* reaches only about 9.4 in (24 cm) in length and is one of the smallest known species of sharks. Ground sharks have two spineless dorsal fins (one species, *Pentanchus profundicolus*, with only one), the first larger than the second. There is a large caudal fin with a greater upper lobe, a prominent anal fin about as large as the pelvic fins (or even larger in some catsharks, especially *Apristurus* species), and moderately developed pectoral fins. There are five gill openings. The snout can be conical or broadly rounded (elongated in *Isogomphodon*). The eyes are elliptical, but they are rounded in some genera (e.g., *Rhizoprionodon*). The spiracles vary from a small pore to an opening just smaller than the eyes. When present, labial furrows (grooves alongside the mouth corners) vary from long to short. There is either a spiral or a scroll intestinal valve. The teeth may vary considerably between adults and juveniles of the same species, upper and lower jaws, and males and females and between species, genera, and families. A single broad, slanted, or erect cusp may be present, or there may be as many as five cusps per tooth (Proscylliidae). Many species are identified by their dental morphological features and formulas. The body is covered with small dermal denticles that do not form larger spines.

Carcharhiniforms vary widely in coloration. Shallow-water catsharks can be spectacularly colored, with many spots, saddle-like markings, and blotches, whereas deeper-water catsharks usually are drab or dark brown or black. Many species (requiem and hammerhead sharks) are gray or brown dorsally and laterally, with creamy or white ventral surfaces. Many triakids also are spotted or have other conspicuous markings similar to those of scyliorhinids. Many ground shark species have unique coloration.

Distribution

They are found worldwide in tropical to temperate waters, including cool boreal seas, but they are most abundant in tropical and warm temperate regions. Carcharhiniform sharks inhabit all major oceans except the Antarctic seas. (Deepwater catsharks of the genus *Apristurus* may inhabit Arctic waters.) They also are present in tropical freshwaters (rivers and lakes) in South, Central, and North America; Africa; Asia; and Australia.

Habitat

Carcharhiniforms are most abundant in tropical continental shelf regions. Most inshore, littoral habitats, including coasts, estuaries, river mouths, open bays and lagoons, atolls, and coral reefs (both coastal and barrier reefs), are occupied by ground sharks. They also are abundant offshore, off oceanic and continental islands, and are present in deeper waters along the upper continental slopes (especially species of *Apristurus* and *Pseudotriakis*). Some species are epipelagic in deeper ocean basins.

Behavior

Carcharhiniform sharks are present in many habitats, from the littoral to the oceanic; as a consequence they vary from sluggish, primarily bottom dwellers (such as many catsharks) to swift swimming, more active pelagic forms (e.g., blue shark and oceanic whitetip shark). The behavior of certain ground shark species has been studied in both captive and natural conditions (in particular, the lemon, gray reef, and bonnethead sharks). In general, pelagic species appear to cruise at low speeds, occasionally bursting into sudden activity, while bottom-dwelling species are more territorial and mostly nocturnal.

Some carcharhiniform species form aggregations, often by size or sex (except during mating season). Schooling is a very

common social behavior in hammerhead sharks (e.g., the scalloped hammerhead, *Sphyrna lewini*, off the eastern Pacific coast of Mexico, where some 225 individuals may school together), but most carcharhiniforms spend much of their lives alone. Gray reef sharks (*Carcharhinus amblyrhynchos*) form schools in the Marshall Islands, as do lemon sharks (*Negaprion brevirostris*) in the Bimini Islands, Bahamas. Schools typically form during the day and break up for individuals to feed at night. Additionally, some species are now known to rest in caves for long periods; the whitetip reef shark, *Triaenodon obesus*, rests mostly during the day and sometimes in groups.

Sharks spend much of their lives as solitary predators and do not form family groups or cooperate with each other. Their types of behavior are less complex than those of marine mammals, but only a handful are known. In particular, aggressive display has been documented (e.g., for the gray reef shark), which may involve jerky head movements, arching of the back, and downward pointing of the pectoral fins. Social displays and social organization are particularly well known for the bonnethead, *Sphyrna tiburo*. Some of these displays are an outcome of size-dependent dominance hierarchies, such as swimming in a straight line. Bonnetheads do not show much aggressive behavior, a possible indication that more social species may be less aggressive.

Feeding ecology and diet

Ground sharks are voracious predators; none are filter feeders. Food items consist of numerous families of bony fishes, sharks and rays, marine mammals and marine mammal carrion, seabirds, marine reptiles (mostly turtles), and a wide range of invertebrates, including crustaceans, squid, octopi, cuttlefish, and shelled mollusks. Benthic ground sharks feed on items more readily available on or close to the bottom, such as hard-shelled invertebrates and certain fishes, whereas open-ocean forms feed intensely on pelagic fishes, such as tunas and their allies (Scombridae). Larger sharks prey on ground sharks, and larger species of ground sharks may feed on smaller ones. The tiger shark has the least selective diet of all sharks. Most species are not highly specialized in their feeding habits, but hammerheads are known to have a particular predilection for stingrays.

A scalloped hammerhead shark (*Sphyrna lewini*) swimming at night in Kanohe Bay, Hawaii. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

A copper shark (*Carcharhinus brachyurus*) near North Neptune Island, Australia. The shark is frequently found near Australia, but has been seen in the waters surrounding all continents except Antarctica. (Photo by Animals Animals ©James Watt. Reproduced by permission.)

Reproductive biology

Carcharhiniform sharks are either oviparous (egg layers) or viviparous (giving birth to live young). Oviparous species deposit egg cases that contain the developing embryo along with its yolk reserves (in the yolk sac). These species include the majority of the catsharks (Scyliorhinidae, except *Cephalurus* and possibly some *Halaelurus* species) and *Proscyllium habereri* (Proscylliidae). The egg cases are secreted by the nidamental gland in the upper oviduct and usually are amber to greenish in color, with tendrils at the extremities that serve to anchor them to the substrate. In species with retained oviparity, the egg cases remain for a longer period in the uterus, with most embryonic development taking place inside the mother. In other oviparous species, the eggs are laid shortly after they are formed (less than one month in some cases), and most development of the fetus, which may take up to one year, occurs inside the egg cases in the environment.

Slightly more than half of carcharhiniform species are viviparous. Viviparous species can be yolk sac viviparous (ovoviviparous or aplacentally viviparous—the young deriving nourishment solely from the yolk sac, such as in the tiger shark, *Galeocerdo*), but many viviparous species form maternal-fetal connections in the form of yolk sac placentae. In these cases, the yolk sacs are modified into highly vascularized, nutrient-supplying structures fused to the internal uterine walls. Placentae are formed in the Hemigaleidae, Carcharhinidae (except *Galeocerdo*), Sphyrnidae, and some triakid species.

Gestation periods vary considerably; oviparous species lay eggs after a short gestation of just a few weeks, but some viviparous species retain the embryos for more than a year.

Gray reef sharks (*Carcharhinus amblyrhynchos*) tend to be gregarious rather than solitary. (Photo by Animals Animals ©James Watt. Reproduced by permission.)

Litters vary from one to 135 per gestation. In many species, females give birth in shallow nursery areas. Males bite females during courtship, and mating has been observed in the wild for a few species (such as the whitetip reef shark, *Triaenodon obesus*). There is no parental care after birth.

Conservation status

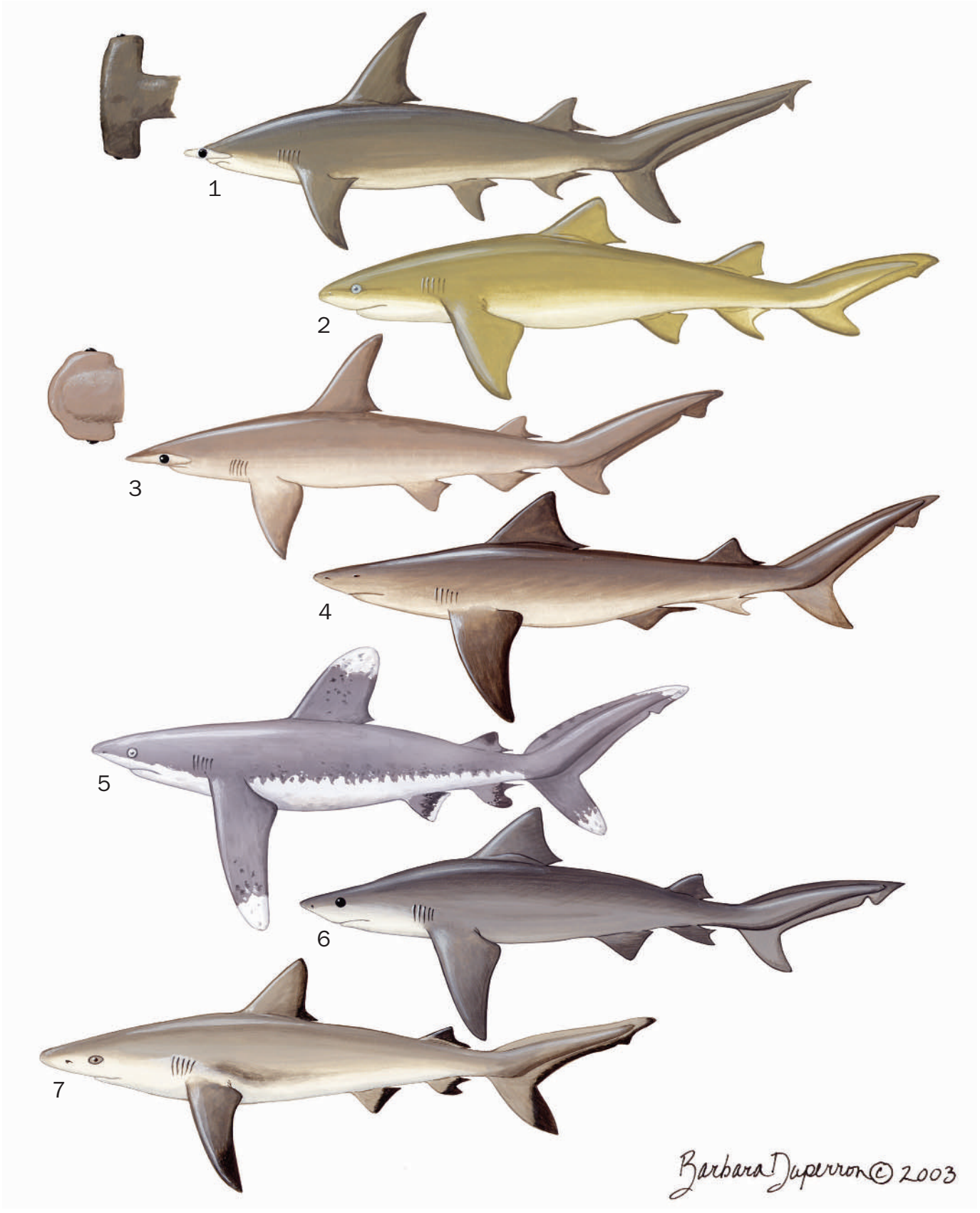
The following species are listed by the IUCN: *Glyphis gangeticus* (as Critically Endangered); *Carcharhinus melanopterus*, *C. borneensis*, and *Glyphis glyphis* (as Endangered); *Galeorhinus galeus* (as Vulnerable); *Mustelus antarcticus* (as Lower Risk/Conservation Dependent); *C. amboinensis* (southwestern Indian Ocean subpopulation only), *C. amblyrhynchoides*, *C. amblyrhynchos*, *C. brevipinna*, *C. leucas*, *C. limbatus*, *C. longimanus*, *C. melanopterus*, *C. obscurus*, *C. plumbeus* (northwestern Atlantic subpopulation only), *Furgaleus macki*, *Galeocerdo cuvier*, *Negaprion brevirostris*, *Poroderma africanum*, *Prionace glauca*, *Scoliodon laticaudus*, *Triaenodon obesus*, *Triakis megalopterus*, and *T. semifasciata* (as Lower Risk/Near Threatened); *C. brevipinna* (northwestern Atlantic subpopulation only), *C. hemiodon*, *C. limbatus* (northwestern Atlantic subpopulation only), *C. obscurus* (northwestern Atlantic and Gulf of Mexico subpopulation only), and *Galeorhinus galeus* (as Vulnerable); and *C. amboinensis* and *Smyrna mokarran* (as Data Deficient).

Significance to humans

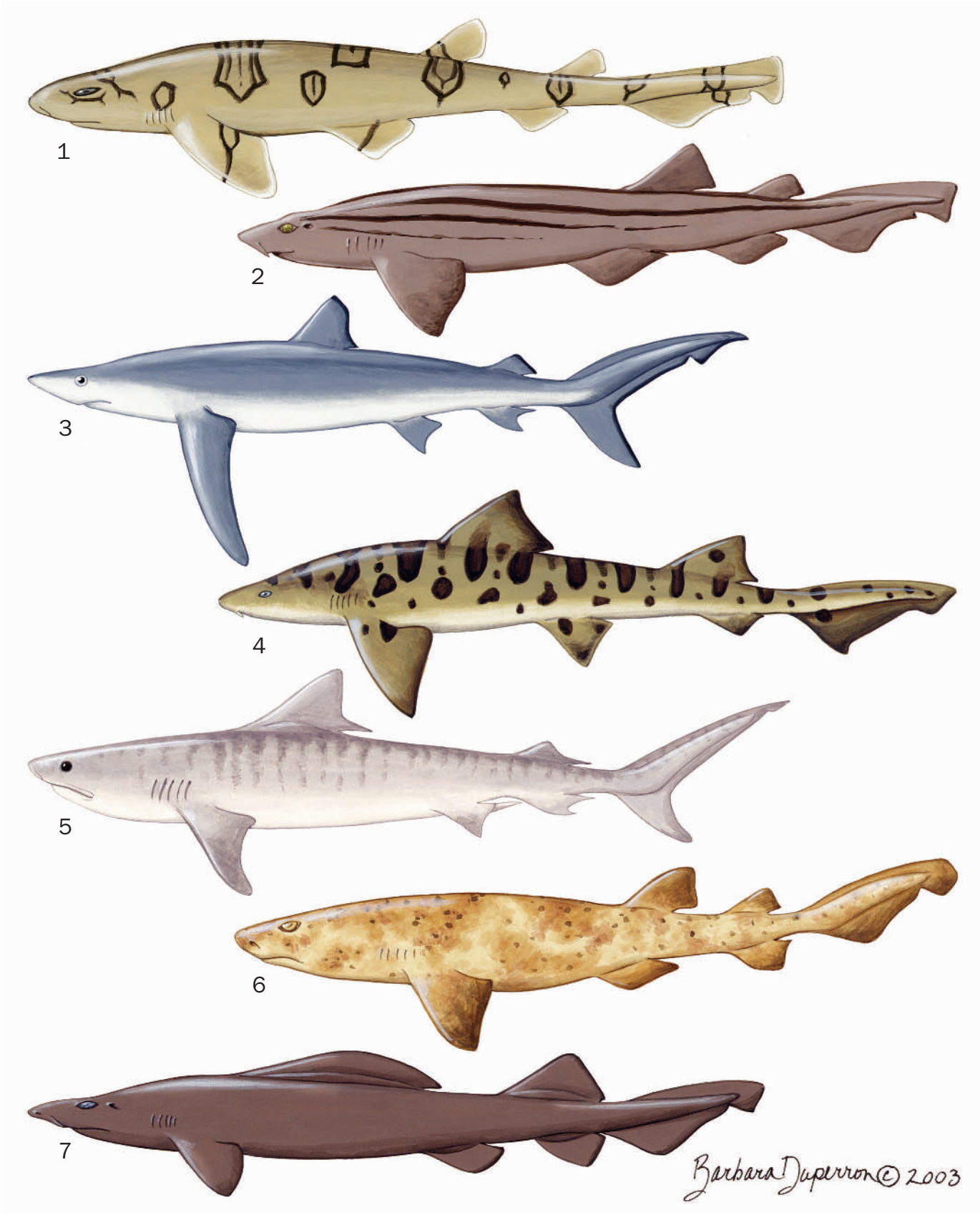
Ground sharks are fished intensely, both for food and recreationally. Because they are abundant in shallow and oceanic waters, ground sharks frequently are fished by trawlers and longlines and are either targeted directly or captured as bycatch. Their flesh is marketed frozen, fresh, dried-salted, smoked, and even canned for human consumption. Their skin is used for leather products, their fins for the Chinese shark fin soup industry, their carcasses for fishmeal, and their liver oil for the extraction of vitamin A (in decline as vitamins are synthesized). Tourists often procure trophies, in the form of jaws and teeth. Recreational fisheries and angling tournaments capture large quantities of ground sharks, especially tiger sharks in shallow waters and blue sharks in oceanic settings. Internal fertilization, long gestation periods, production of few offspring, and relatively advanced ages at sexual maturity are all factors that constrain the exploitation of shark populations.

Ground sharks have been implicated in numerous shark attacks, especially the tiger and bull sharks, which account for more than 50% of shark attacks worldwide. This proportion is to be expected because of the high number of carcharhiniform species and their shallow-water predominance.

Carcharhiniforms also are very important in the growing ecotourism market. Many species can be encountered in the wild through commercial operations that specialize in taking tourists to areas where specific carcharhiniform species are common. These operations are worldwide, and surveys indicate that shark watching is a highly profitable enterprise. Certain ground shark species are common in public aquaria as well, especially *Triaenodon obesus*, *Carcharhinus plumbeus*, and *Triakis semifasciata*.



1. Great hammerhead shark (*Sphyrna mokarran*); 2. Lemon shark (*Negaprion brevirostris*); 3. Bonnethead shark (*Sphyrna tiburo*); 4. Ganges shark (*Glyphis gangeticus*); 5. Oceanic whitetip shark (*Carcharhinus longimanus*); 6. Bull shark (*Carcharhinus leucas*); 7. Gray reef shark (*Carcharhinus amblyrhynchos*). (Illustration by Barbara Duperron)



1. Chain catshark (*Scyliorhinus retifer*); 2. Pajama (*Poroderma africanum*); 3. Blue shark (*Prionace glauca*); 4. Leopard shark (*Triakis semifasciata*); 5. Tiger shark (*Galeocerdo cuvier*); 6. Swellshark (*Cephaloscyllium ventriosum*); 7. False catshark (*Pseudotriakis microdon*). (Illustration by Barbara Duperron)

Species accounts

Gray reef shark
Carcharhinus amblyrhynchos

FAMILY
Carcharhinidae

TAXONOMY
Carcharias (Prionodon) amblyrhynchos Bleeker, 1856, Java Sea, near Salambo Islands, Indonesia.

OTHER COMMON NAMES
French: Requin dagsit; Spanish: Tiburón de arrecifes.

PHYSICAL CHARACTERISTICS
Somewhat elongated snout but with a rounded anterior profile, first dorsal fin much larger than the second, and rounded eyes. Upper teeth have posteriorly slanted cusps with faint serrations; lower teeth are slender and more erect. Coloration is grayish dorsally and laterally, but with a distinctive black caudal fin margin. Reaches some 8 ft (2.5 m) in length.

DISTRIBUTION
Occurs in mostly tropical waters of the Indian and Pacific Oceans.

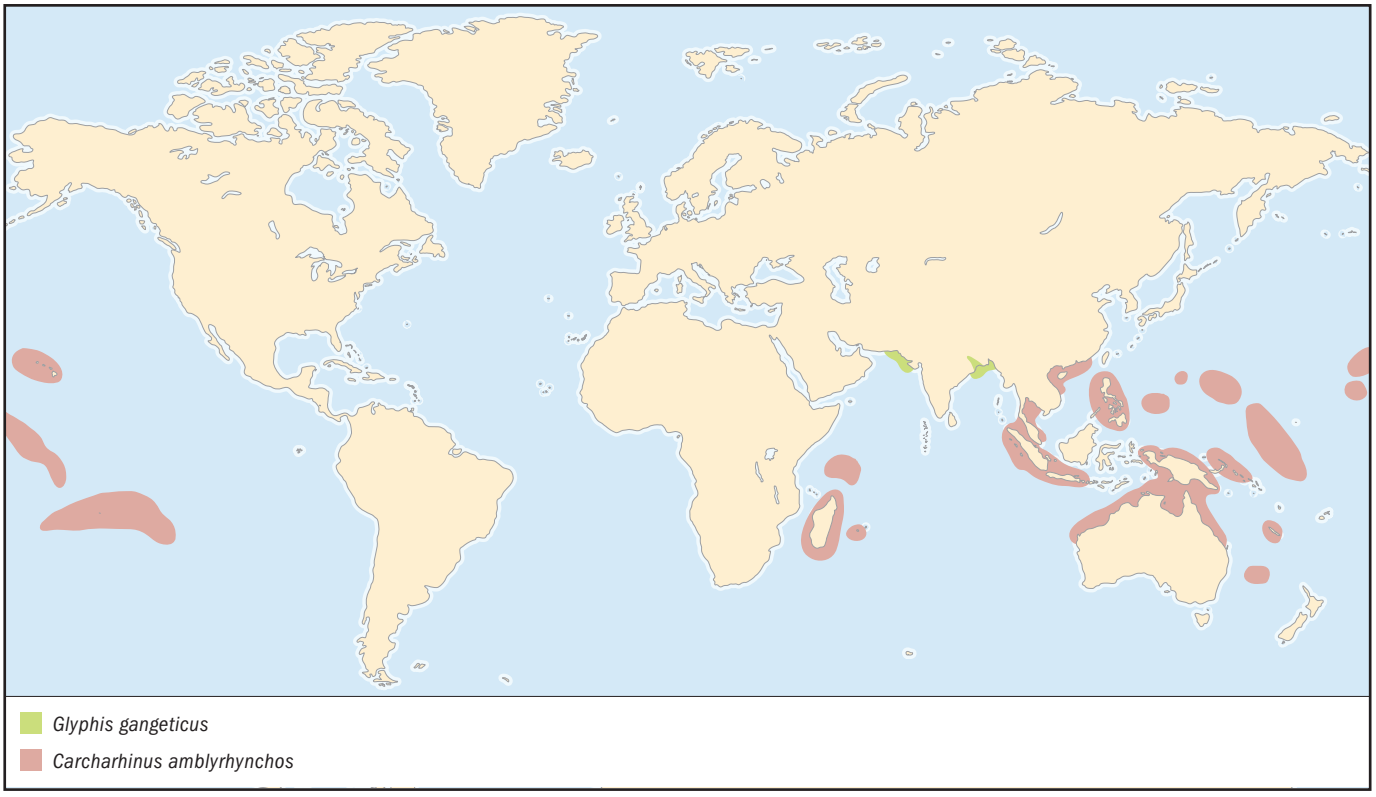
HABITAT
An inshore shark but also occurs pelagically and sometimes frequents oceanic waters from the intertidal zone down to about 330 ft (100 m). A common species in coral reefs, atolls, and shallow lagoons. Usually found close to the bottom but also may be seen near the surface.

BEHAVIOR
A curious shark that investigates "novel" circumstances while swimming. Approaches divers frequently but typically disappears shortly thereafter. Can be aggressive when in pursuit of prey. A particular threat display has been observed and documented, in which the gray reef shark arches its back, points its pectorals downward, lifts its head, moves its snout from side to side repeatedly, and even swims in a horizontal spiral. Considered to be a very social species.

FEEDING ECOLOGY AND DIET
Feeds on bony fishes (especially those that inhabit reefs and are shorter than 12 in, or 30 cm), octopi, squid, and a wide variety of crustaceans. Notable for being able to capture prey in tight crevices in reefs.

REPRODUCTIVE BIOLOGY
Viviparous, with a yolk sac placenta and litters raging from one to six young. Gestation period is about one year. Individuals are sexually mature by seven to seven and a half years old. Males are mature at a length of 51–57 in (130–145 cm) and females when they reach 48–54 in (122–137 cm).

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN because of its relatively late age at maturity and increasing pressure from unmanaged fishing.



SIGNIFICANCE TO HUMANS
A very common reef shark, with great potential for dive tourism, as is readily seen by ecotourists in many locations (e.g., Australia, Mauritius, and the Philippines). Fishing and utilization mostly unrecorded. ◆

Bull shark
Carcharhinus leucas

FAMILY
Carcharhinidae

TAXONOMY
Carcharias (Prionodon) leucas Valenciennes in Müller and Henle, 1839, Antilles.

OTHER COMMON NAMES
French: Requin bouledogue; Spanish: Tiburón sarda; Portuguese: Cabeça-chata.

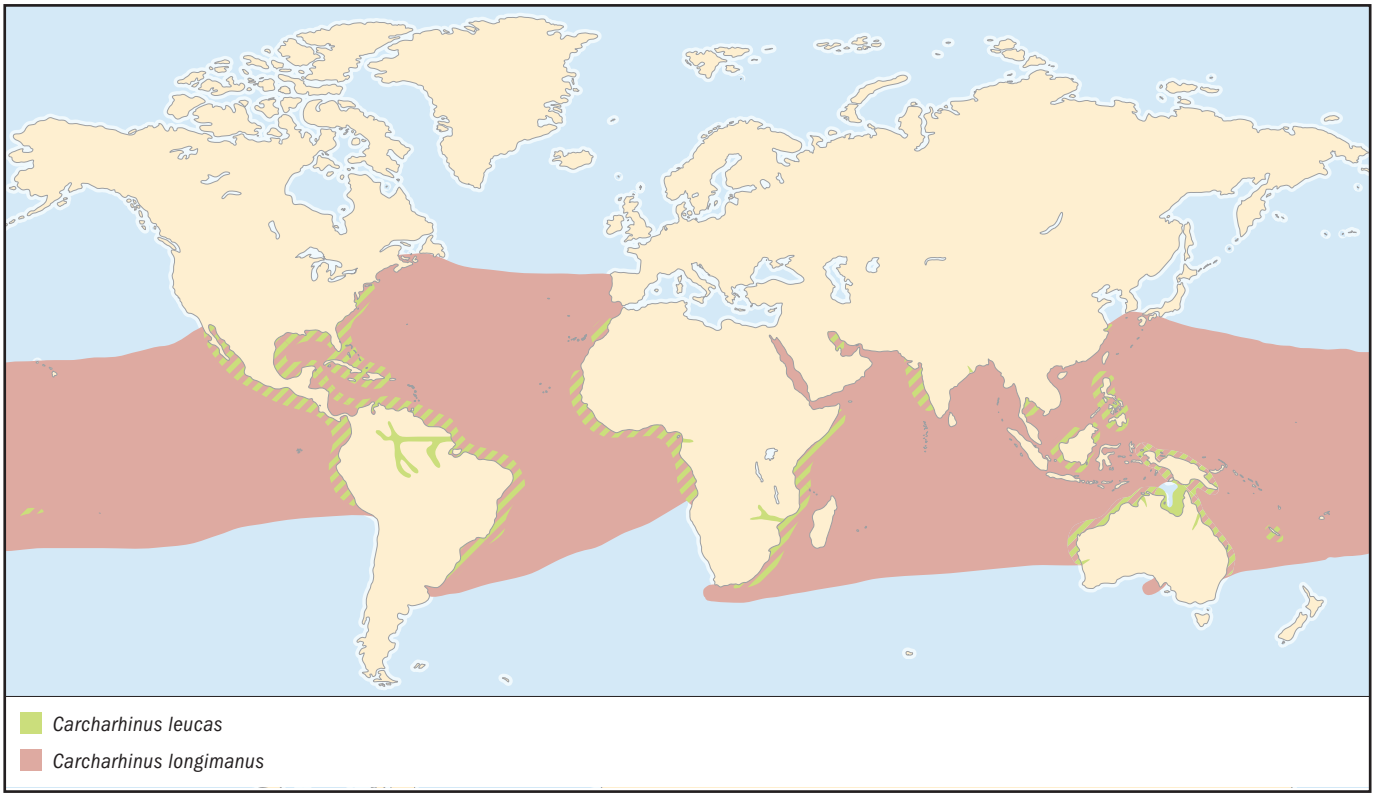
PHYSICAL CHARACTERISTICS
Characteristically short and blunt snout, somewhat arched back, and relatively small eyes. Large first dorsal fin (much larger than the second dorsal fin). Triangular upper teeth with small cusplets. Upper teeth more broad than lower teeth, which are smooth laterally. Thirteen upper tooth rows and 12 lower rows. Gray to brownish dorsal and lateral coloration. Reaches 11.5 ft (3.5 m) in length.

DISTRIBUTION
Worldwide in tropical shallow waters but also ascending tropical rivers and freshwater lakes. Freshwater occurrences include the Amazon and Ucayali Rivers in South America, reaching upriver as far as 2610 mi (4,200 km) from shore); the Mississippi and Atchafalaya Rivers of the United States; Lake Nicaragua and San Juan River (Nicaragua); Lake Izabal and Dulce River (Guatemala); and the Patuca River (Honduras). Also in freshwaters in Belize and probably elsewhere in other neotropical systems. Other freshwater occurrences include many African rivers (Gambia, Ogooué, and Zambezi Rivers), Middle Eastern rivers (the Tigris), Indian waters (Hooghly Channel of the Ganges River), New Guinea waters (Lake Jamoer), and systems in Australia (Brisbane River). Present in some oceanic islands (Fiji).

HABITAT
In the sea the bull shark is widespread in inshore, shallow waters, frequenting bays, estuaries, river mouths, and waters off piers and docks, usually down to a depth of 98.4 ft (30 m) but reaching 492 ft (150 m). Its capacity to penetrate freshwaters extensively and remain in them, tolerating great ranges in salinity, has been the subject of much scientific research. Freshwater populations are not believed to be landlocked, however, and migrate frequently to the sea, such as in the Lake Nicaragua system.

BEHAVIOR
Active both during the day and at night. May aggregate to migrate to cooler waters in the summer from equatorial latitudes, returning when water temperatures become too cool. Smaller, younger individuals may be more common close to shore, whereas larger individuals may inhabit slightly deeper waters. Appears somewhat sluggish but is capable of swift movements and sudden bursts of activity.

FEEDING ECOLOGY AND DIET
Feeds extensively on many different bony fishes as well as sharks and rays but is capable of consuming a wide range of



prey, including invertebrates and marine mammals, reptiles, and birds.

REPRODUCTIVE BIOLOGY
Viviparous with a yolk sac placenta; litters range from one to 13 young. Gestation periods range from 10 to 11 months. Breeding in freshwaters may occur (e.g., in Lake Nicaragua), but most breeding takes place in the sea. Sexual maturity is attained at about 98.4 in (250 cm) in length, after some six years. Pups frequently are born in sheltered nursing areas. Lengths at birth range from roughly 19.7 to 31.5 in (50–80 cm).

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, mainly because of its occurrence close to heavily populated areas and frequency of capture by local fisheries.

SIGNIFICANCE TO HUMANS
A hardy aquarium species; individuals have lived for 15 years. Captured as bycatch by fisheries in many places, leading to a concern that the bull shark may be threatened in some areas. Its meat is consumed fresh, dried/salted, and smoked, and its liver is particularly rich in oil. Also captured recreationally on hook and line in many regions. Considered a dangerous shark, with many attacks reported. It is believed that some attacks are caused by other species, such as the great white in temperate waters and the Ganges shark in the Ganges-Hooghly river system. Some attacks have occurred in freshwater (e.g., in Lake Nicaragua). The bull shark can be encountered in the wild in many places worldwide (e.g., the Bahamas, Cuba, and Belize). ◆

Oceanic whitetip shark
Carcharhinus longimanus

FAMILY
Carcharhinidae

TAXONOMY
Squalus longimanus Poey, 1861, Cuba.

OTHER COMMON NAMES
French: Requin océanique; Spanish: Tiburón oceánico.

PHYSICAL CHARACTERISTICS
Short and blunt snout. First dorsal fin is characteristically large, with a unique, broadly rounded apex; pectoral fins are long and also unique, with broadly rounded apex. Small second dorsal fin and large caudal fin. Broad upper teeth that are triangular with lateral serrations; lower teeth have straight, slender cusp. Gray dorsal and lateral color, with uniquely white extremities of pectoral and first dorsal fins, sometimes with darker blotches. Second dorsal, pelvic, anal, and caudal fins have dark tips; caudal extremities sometimes also white. Reaches 13 ft (4 m) in length.

DISTRIBUTION
Worldwide in tropical and temperate inshore and oceanic waters.

HABITAT
Typically occurs close to the surface, in offshore oceanic waters but may venture close to shore occasionally in waters as shallow as 121 ft (37 m). More abundant in the tropics.

BEHAVIOR
May segregate by sex and size, but little is known of its population structure. Slow moving but capable of quick bursts of energy. Oceanic whitetips appear to cruise with their pectoral fins widely spread out. Inquisitive, the oceanic whitetip will investigate potential prey items by circling them repeatedly.

FEEDING ECOLOGY AND DIET
Feeds on oceanic bony fishes of numerous families as well as on sharks and pelagic stingrays and invertebrates, such as oceanic cephalopods. Has been noted to feed voraciously on schools of fish. Also may feed on marine mammal carrion, seabirds, and turtles.

REPRODUCTIVE BIOLOGY
Viviparous, with a yolk sac placenta and litters ranging from one to 15 young. Gestation periods of about one year have been reported, but little is known about the reproductive biology. Reproductive seasons may not strictly exist, at least in the central Pacific, where gravid females have been found year-round. Lengths at sexual maturity are between 71 and 78.7 in (180–200 cm) for females and 69 and 78 in (175 to 198 cm) for males; lengths at birth vary from 23.6 to 25.6 in (60–65 cm).

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, because it is captured frequently as by-catch in pelagic tuna fisheries and owing to its presumably low reproductive capacity.

SIGNIFICANCE TO HUMANS
A few verified attacks on people have occurred, and the oceanic whitetip has been regarded as somewhat aggressive when approaching divers or boats. Regularly captured by pelagic longlines. The flesh is consumed fresh, dried/salted, and smoked, and the fins are coveted by the shark fin soup industry. Can be seen in the waters off Hawaii, the Red Sea, and Australia. ◆

Tiger shark
Galeocerdo cuvier

FAMILY
Carcharhinidae

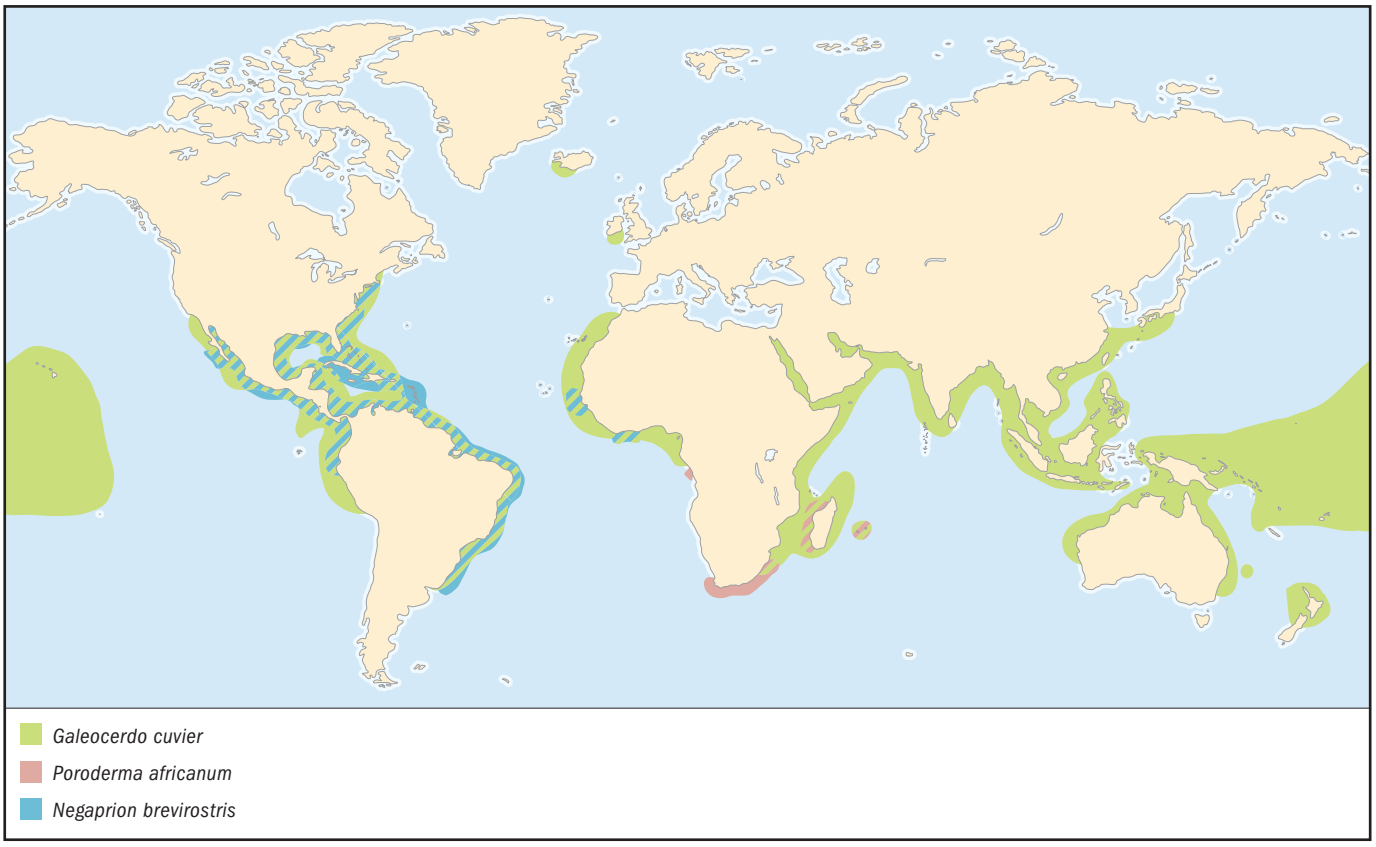
TAXONOMY
Squalus cuvier Peron and LeSuer, 1822, Australia.

OTHER COMMON NAMES
French: Requin tigre commun; Spanish: Tintorera.

PHYSICAL CHARACTERISTICS
Characteristically short and rounded snout. A large first dorsal fin (well anterior to the pelvic fin origin), well-developed caudal fin, and long upper labial furrows. Unique teeth, with posteriorly curved and serrated cusps. Coloration of dark vertical stripes (more apparent in juveniles) over a gray background. Large females reach 19.7 ft (6 m) in length, with unconfirmed records of up to 29.5 ft (9 m).

DISTRIBUTION
Worldwide in tropical to warm temperate, mostly continental waters but may occur pelagically in the western Pacific Ocean.

HABITAT
The tiger shark is mainly an inshore, warm-water species, occurring in continental waters as well as in remote oceanic islands from the intertidal zone down to about 459 ft (140 m). Very common in turbid waters, off river estuaries, near piers, and in coral reefs. May be found pelagically offshore but is not a truly oceanic shark like the blue shark.



BEHAVIOR
A mostly nocturnal, active, and strong-swimming species, capable of frequenting very shallow lagoons. Usually solitary. Appears sluggish because it cruises at slow speeds near the surface. Can approach and display aggressive behavior toward divers, but in many instances tiger sharks have been turned away by strong retaliation.

FEEDING ECOLOGY AND DIET
Feeds on a wide variety of vertebrates and invertebrates, and is considered among the least specialized of sharks in relation to diet, scavenging opportunistically as well as being a top marine predator. Tiger sharks also have been known to ingest inedible objects (license plates, plastics, cans, and an amazing variety of trash). Prey items vary from large fishes (many sharks and rays as well as larger bony fishes, such as tarpon), marine reptiles, mammals, and birds to mollusks (octopi, squid, and cuttlefish) and crustaceans. Actively attacks birds resting on the surface, lifting its massive head out of the water to bite down on them as they attempt to escape.

REPRODUCTIVE BIOLOGY
Aplacentally viviparous. (The only member of its family in which maternal-fetal connections do not form.) Gestation is slightly longer than one year. Gives birth to 10–82 rather large young (20.1–29.9 in [51–76 cm]). Inshore nursing grounds are common. Matures sexually between four and six years old.

CONSERVATION STATUS
Considered to be Lower Risk/Near Threatened by the IUCN, as there is some evidence that several populations have declined where they are heavily fished.

SIGNIFICANCE TO HUMANS
Considered in many places to be a dangerous shark—many attacks on people and boats have been attributed to this species in tropical seas. Commonly hooked by fishermen and captured by longlines. The meat is utilized fresh, dried/salted, or frozen; the skin for leather; the fins for soup; and the oily liver processed for vitamin oil. Fished recreationally as well. Remains alive in aquaria for only short periods, not surpassing a few months. The tiger shark may be seen in the wild in Hawaii, Australia, and the Rangiroa Atoll (French Polynesia). ◆

Ganges shark
Glyphis gangeticus

FAMILY
Carcharhinidae

TAXONOMY
Carcharias (Prionodon) gangeticus Müller and Henle, 1839, Ganges River.

OTHER COMMON NAMES
French: Requin du Ganges; Spanish: Tiburón del Ganges.

PHYSICAL CHARACTERISTICS
Snout rounded anteriorly, with very small eyes, large first dorsal fin well anterior to pelvic fin origin, large pectoral and caudal fins, small upper labial furrow, upper jaw teeth broadly triangular with minute serrations, lower jaw teeth very acute

and slender with smooth edges. Gray coloration dorsally and laterally and white ventrally. Reaches more than 6.6 ft (2 m) in length.

DISTRIBUTION
Hooghly Channel of the Ganges River (India).

HABITAT
A freshwater species, the notorious Ganges shark is known from only two surviving specimens collected in the Ganges River. Its small eyes may indicate that this species lives exclusively in the murky Ganges. Needs confirmation by means of additional specimens from the Ganges and surrounding areas; unknown whether it is capable of tolerating marine waters.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumably fishes, but presently unknown.

REPRODUCTIVE BIOLOGY
Unknown, but presumably reproduces in freshwater, as indicated by a newly born male specimen, 25.6 in (65 cm) long, collected from the Hooghly Channel of the Ganges River.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN because of the paucity of specimens and information and considered at extreme risk of extinction.

SIGNIFICANCE TO HUMANS
The Ganges shark has an unproven, folkloric reputation as a "man-eater" in the Ganges River. As the bull shark (*Carcharhinus leucas*) also occurs there, many of the attacks attributed to the Ganges shark may be a result of misidentification. The Ganges shark is one of the least known and most mysterious shark species. It is known originally from three museum specimens, collected from freshwaters of the lower reaches of the Ganges-Hooghly river system in the nineteenth century, but of which only one is extant. An additional specimen was found subsequently in India (the newly born male mentioned previously), but no further confirmed specimens are known. ◆

Lemon shark
Negaprion brevirostris

FAMILY
Carcharhinidae

TAXONOMY
Hypoprion brevirostris Poey, 1868, Cuba.

OTHER COMMON NAMES
French: Requin citron; Spanish: Tiburón galano.

PHYSICAL CHARACTERISTICS
Somewhat rounded and blunt snout, no labial furrows, first dorsal fin well anterior to pelvic fin origin, relatively large second dorsal and anal fins, and moderately large caudal fin. Teeth have slender, smooth, and triangular cusps. Coloration is gray to yellowish-brown dorsally and laterally, creamy white ventrally. Reaches about 11.5 ft (3.5 m) in length.

DISTRIBUTION
Tropical and warm temperate waters. Present in the eastern Pacific off the coasts of Mexico south to Peru; in the western Atlantic from New England to southern Brazil, Gulf of Mexico, and Caribbean; and in the eastern Atlantic off Senegal and probably elsewhere in Africa.

HABITAT
An inshore, coastal species common in coral reefs, mangroves, and bays; around piers and docks; and at river mouths, occurring from the surface down to about 328 ft (100 m). May penetrate freshwater but not only for short distances.

BEHAVIOR
Lemon sharks are active both during the day and at night, with peaks of activity at dawn or dusk. They prefer shallow areas, and individuals may display site preferences, especially younger sharks. Their home range expands with growth, as young sharks may remain within a region encompassing 3.7–5 mi^2 (6–8 km^2), which may expand to 186 mi^2 (300 km^2) when they reach adulthood. Lemon sharks may remain active in low-oxygen environments because of their high respiratory efficiency. They typically are found resting on the bottom. Adults may undertake long seasonal migrations.

FEEDING ECOLOGY AND DIET
Feeds mostly on fishes (including many different rays), crustaceans, and mollusks. Also may consume seabirds occasionally. Young lemon sharks, 27.6 in (70 cm) in length, have been able to eat 3% of their body weight in captivity, with unlimited food available.

REPRODUCTIVE BIOLOGY
A viviparous species with a yolk sac placenta. Litters commonly have between four and 17 young, and gestation periods last from 10 to 12 months. Young are born in shallow nursery areas and remain there for a short period. Sexual maturity is reached after about six and a half years. Both courtship and mating have occurred in captivity.

CONSERVATION STATUS
Listed as Lower Risk by the IUCN, because young specimens inhabit coastal nursery regions that may be subject to development and habitat degradation.

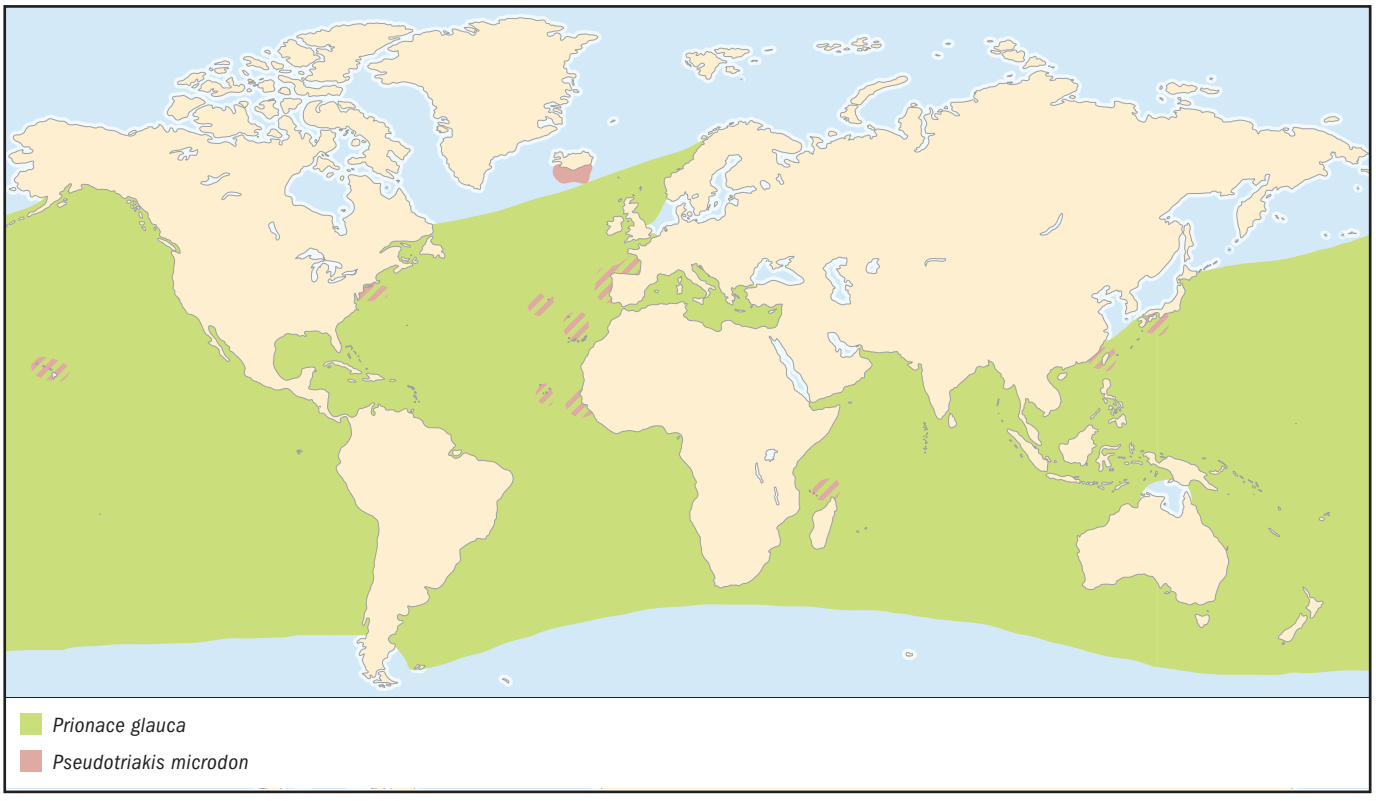
SIGNIFICANCE TO HUMANS
A hardy species in captive conditions. Caught frequently on longlines and fished by anglers. The flesh may be consumed fresh or in other ways. There is evidence of population declines in the eastern Pacific and western Atlantic. Attacks on people have been recorded, largely owing to the lemon shark's preference for shallow water in areas that are heavily populated. The lemon shark, however, is not considered an aggressive species. May be seen in the wild in the Bahamas, Turks and Caicos, Florida, Belize, and many other Caribbean locations. ◆

Blue shark
Prionace glauca

FAMILY
Carcharhinidae

TAXONOMY
Squalus glauca Linnaeus, 1758, "Oceano Europaeo."

OTHER COMMON NAMES
French: Peau bleu; Spanish: Tiburón azul.



PHYSICAL CHARACTERISTICS
The blue shark has characteristically long pectoral fins, a slender body with a large caudal fin, an elongated snout, widely separated dorsal fins, and first dorsal fin much larger than the second. Teeth have small lateral serrations and are slightly different in the upper and lower jaws. Deep blue dorsal coloration, with lighter blue sides and white ventrally. Reaches some 13 ft (4 m) in length.

DISTRIBUTION
Worldwide in tropical and temperate waters. It is perhaps the widest-ranging chondrichthyan.

HABITAT
The blue shark is an oceanic, epipelagic shark that enters littoral regions with frequency. Usually found close to the surface but has been captured at depths slightly more than 722 ft (220 m) in warmer latitudes.

BEHAVIOR
May occur in loosely organized aggregations, cruising at slow speeds close to the surface, but capable of swift bursts of speed; may even jump out of the water. Known to circle potential prey items before attacking. May migrate seasonally, and tagged individuals have been recaptured at very distant locations (e.g., across the Atlantic). May bite objects or potential prey out of curiosity or in an attempt to "taste" them before committing to a feeding. Blue sharks are capable of making sharp, quick turns, an indication of their extreme versatility.

FEEDING ECOLOGY AND DIET
Consumes mostly pelagic bony fishes, and especially squid, that occur close to the surface but also may feed on other sharks (such as the piked dogfish, *Squalus acanthias*, and, in one case, the goblin shark, *Mitsukurina owstoni*), invertebrates, mammalian carrion, and even seabirds. Feeds massively on squid during breeding aggregations and on flying-fish eggs during spawning in the Adriatic.

REPRODUCTIVE BIOLOGY
Viviparous with a yolk sac placenta; litters range from four to 135 young (the greatest range of any live-bearing shark). Gestation is from nine to 12 months. Sexual maturity is reached after some five years (slightly younger for males). Females are sexually mature at about 86.6 in (220 cm) in length, males at slightly smaller sizes. Females store sperm in the shell glands of their oviducts after copulation (which usually takes place from late spring to early winter in temperate regions and all year in tropical seas), utilizing it only when their ovaries ripen to produce and release eggs into the oviduct. Sperm may be stored in this manner for a period of one year. Courtship rituals involve biting, and the sexes can be distinguished readily according to the presence of scars on the body. Females may have skin three times as thick as males. Individuals may segregate by sex.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, mostly owing to the lack of data concerning the effects of presently being the most fished shark species in the world and an important keystone predator in the oceanic realm.

SIGNIFICANCE TO HUMANS
Heavily fished in much of its range, usually by means of pelagic longlines. Consumed fresh, frozen, and dried/salted. The skin may be used for leather and the fins for shark fin soup. Also fished recreationally. Attacks on people have been attributed to this species, but there also have been many harmless encounters. Nevertheless, the blue shark should be approached with caution. There are many places where tourists may take day trips to see blue sharks in the wild (e.g., California, Portugal, and New Zealand). ◆

False catshark
Pseudotriakis microdon

FAMILY
Pseudotriakidae

TAXONOMY
Pseudotriakis microdon Capello, 1868, Setubal, Portugal.

OTHER COMMON NAMES
French: Requin à longue dorsale; Spanish: Musolón de aleta larga.

PHYSICAL CHARACTERISTICS
A unique shark, with an extremely elongated, low first dorsal fin; a tall, triangular second dorsal fin; a large anal fin, elongated, slitlike eyes; and a wide mouth with 200–300 rows of numerous minute teeth in each jaw. Covered in prickly denticles and with brownish-black coloration. Reaches 9.8 ft (3 m) in length.

DISTRIBUTION
Worldwide in tropical and temperate latitudes.

HABITAT
A deepwater, demersal species, occurring predominantly from 656 to 4,920 ft (200–1,500 m) along the continental slopes. May venture rarely into more shallow waters of the continental shelf.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Largely unknown but presumably consumes demersal fishes and invertebrates. The huge mouth of the false catshark probably allows it to ingest prey of considerable size.

REPRODUCTIVE BIOLOGY
Aplacentally viviparous (ovoviviparous), with small litters (reportedly two to four young) but producing copious numbers of eggs (estimated at 20,000 in one ovary of a female 110 in, or 280 cm, in length).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Not consumed in significant quantities but occasionally captured with bottom longlines. Not considered dangerous. ◆

Swellshark
Cephaloscyllium ventriosum

FAMILY
Scyliorhinidae

TAXONOMY
Scyllium ventriosum Garman, 1880, Valparaíso, Chile.

OTHER COMMON NAMES
Spanish: Pejegato hinchado.

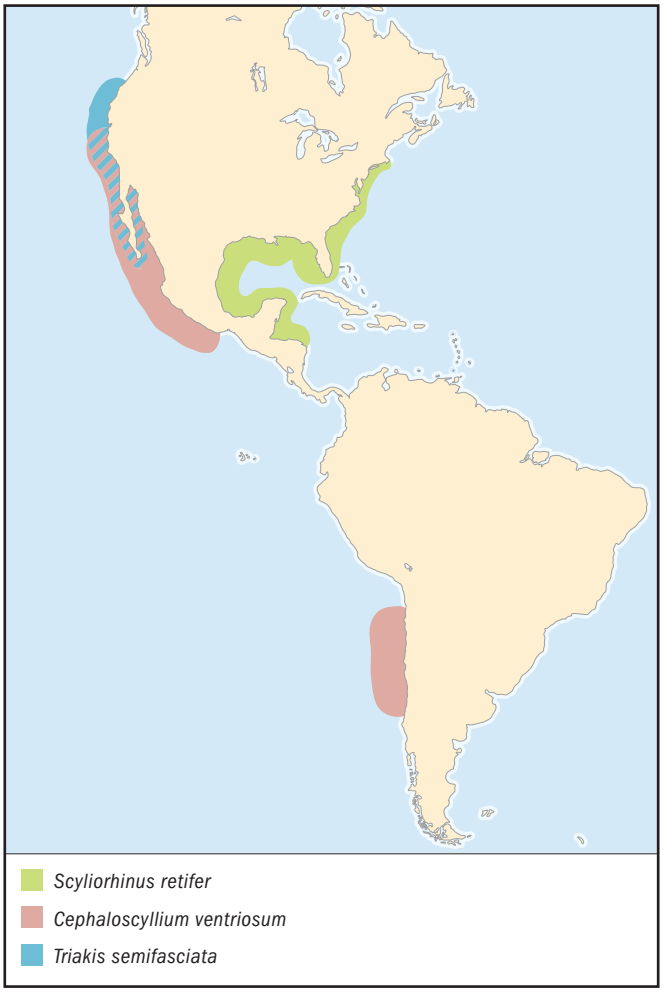
PHYSICAL CHARACTERISTICS
Posterior margins of nasal flaps reaching the mouth, broadly rounded snout. The first dorsal fin behind the origin of the pelvic fins and larger than the second dorsal fin; relatively large anal fin and large eyes. Teeth have small lateral cusplets. Large brown blotches and saddles dorsally and laterally and small darker and lighter spots ventrally and laterally on a yellowish-brown background. Reaches about 3.3 ft (1 m) in length.

DISTRIBUTION
Occurs in the eastern Pacific Ocean from Monterey Bay, California, south to central Chile; not yet recorded from the south of Mexico to southern Peru.

HABITAT
Usually present in shallow waters, from 16.4 to 121.4 ft (5–37 m) but occasionally caught deeper on the upper continental slope, to 1,500 ft (457 m). Found on rocky bottoms but also on substrates covered by algae.

BEHAVIOR
A sluggish shark that remains mostly motionless, sheltered in caves or crevices during the day and becoming more active at night. Individuals may aggregate while resting. As their common name implies, swellsharks are capable of inflating their stomachs with water or air to escape predation (similarly to pufferfishes). They even may wedge themselves in crevices in this manner.

FEEDING ECOLOGY AND DIET
Feeds mostly on bony fishes but also may eat hard-shelled invertebrates.



REPRODUCTIVE BIOLOGY
Oviparous (egg laying), depositing amber to greenish egg cases with smooth surfaces and elongated tendrils. Young hatch after a period of seven and a half to 10 months, at about 5.1–5.9 in (13–15 cm) in length. Young have a row of enlarged denticles along the back that may aid them when leaving the egg cases. Males sexually mature between 32.3 and 33.5 in (82–85 cm) in length.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Swellsharks do well in captivity and are featured in many aquaria. Females even lay egg cases in aquaria. These sharks are not consumed and probably are discarded if captured in trawls. Not considered dangerous to people but may become aggressive if harassed. ◆

Pajama catshark
Poroderma africanum

FAMILY
Scyliorhinidae

TAXONOMY
Squalus africanus Gmelin, 1789, "Mari Africanum," probably off South Africa.

OTHER COMMON NAMES
English: Striped catshark; French: Roussette rubanée; Afrikaans: Streep-kathaai.

PHYSICAL CHARACTERISTICS
An unmistakable shark, with longitudinal, broad stripes from head to tail on the dorsal and lateral sides. Elongated eyes, first dorsal fin posterior to pelvic fin origin and larger than the second dorsal, and relatively short narial barbels. Reaches about 3.3 ft (1 m) in length.

DISTRIBUTION
Found primarily off South Africa but also in the eastern Atlantic near the mouth of the Congo River. Records needing confirmation exist from Madagascar and Mauritius.

HABITAT
A shallow-water, inshore species, occurring in waters down to 328 ft (100 m) deep. Common in caves and over rocky substrates.

BEHAVIOR
A common, mostly nocturnal and somewhat sluggish shark, but behavior is poorly known.

FEEDING ECOLOGY AND DIET
Feeds on crustaceans, cephalopods, polychaetes, and many different bony fishes.

REPRODUCTIVE BIOLOGY
An oviparous species, laying a single egg case per oviduct. One egg laid in an aquarium hatched after five and a half months. Males are sexually mature between 22.8 and 29.9 in (58–76 cm) in length and females between 25.6 and 28.3 in (65–72 cm).

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, because of its restricted occurrence mostly in regions with high levels of human activity and fishing.

SIGNIFICANCE TO HUMANS
Readily kept in aquaria but not consumed or captured significantly. Occasionally captured as by-catch by bottom trawlers but usually discarded; fished recreationally. Not dangerous to people. ◆

Chain catshark
Scyliorhinus retifer

FAMILY
Scyliorhinidae

TAXONOMY
Scyllium retiferum Garman, 1881, off Virginia, United States.

OTHER COMMON NAMES
Spanish: Alitán mallero.

PHYSICAL CHARACTERISTICS
Coloration unique, composed of numerous brown saddles with a conspicuous internal network pattern that also is present over the pectoral and caudal fins. First dorsal fin behind origin of pelvic fins and larger than the second dorsal fin, back somewhat arched. Elongated, slitlike eyes. Reaches about 19.7 in (50 cm) in length.

DISTRIBUTION
Present in the western North Atlantic from southern New England to Florida; found in the Gulf of Mexico from Florida south to Nicaragua.

HABITAT
A mostly deepwater species, demersal on the outer continental shelf to the upper slope region, from 29 to 1,800 ft (73–550 m) in depth.

BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Presumably feeds on fishes and invertebrates, as it lives mostly in close association with the bottom, but full stomach contents have yet to be examined. Cephalopod beaks were found in one specimen.

REPRODUCTIVE BIOLOGY
Oviparous (egg laying), but most details concerning its reproduction are unknown. Males mature sexually at about 14.6–16.1 in (37–41 cm) in length, females from 13.8 to 18.5 in (35–47 cm). Length at birth is about 3.9 in (10 cm).

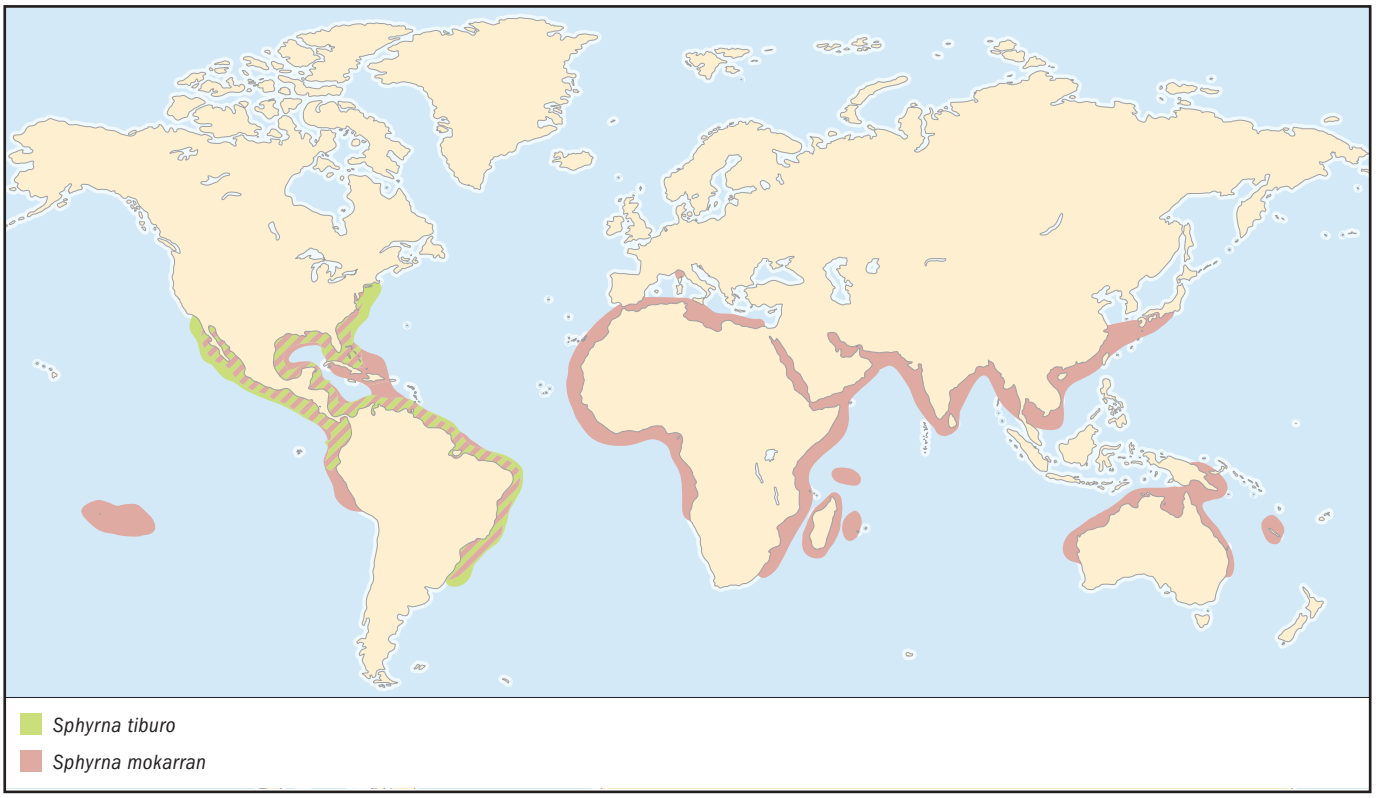
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Captured occasionally as by-catch in bottom trawls but is not consumed and is discarded. Not dangerous, owing to its size and habitat. ◆

Great hammerhead shark
Sphyrna mokarran

FAMILY
Sphyrnidae

TAXONOMY
Zygaena mokarran Rüppel, 1837, Red Sea.



OTHER COMMON NAMES
French: Grand requin-marteau; Spanish: Cornuda gigante.

PHYSICAL CHARACTERISTICS
Cephalofoil (hammerhead) with somewhat straight anterior margin with a slight median indentation. Hammerhead not very broad proportionally. Very tall first dorsal fin entirely anterior to pelvic fin origins, pelvic and anal fins with strongly concave posterior margins, and well-developed caudal fin. Serrated teeth. Uniform gray coloration. The largest of the hammerhead sharks, reaching some 20 ft (6 m) in length.

DISTRIBUTION
Worldwide in coastal tropical to warm temperate waters.

HABITAT
Common in inshore tropical waters but also present offshore, occurring close to the water'surface to depths of 263 ft (80 m).

BEHAVIOR
A nomadic, migratory species, the great hammerhead shark can occur in great numbers, with individuals moving their heads from side to side as they cruise at midwater depth.

FEEDING ECOLOGY AND DIET
Eats a variety of bony fishes but seems particularly fond of stingrays, rays in general, groupers, and marine catfishes. Many fishes are commonly taken as prey (even smoothhound sharks). The venemous stings of stingrays and catfishes do not appear to harm the great hammerhead, as they frequently are found stuck in the mouth and pharynx. (One specimen apparently had more than 50 stings embedded in its mouth, throat, and tongue.) Also may feed on crabs and squid.

REPRODUCTIVE BIOLOGY
Viviparous with a yolk sac placenta and litters ranging from 13 to 42 young. Equal numbers of males and females usually are born. Gestation may last seven months. Males are sexually mature at about 93–106 in (235–269 cm) in length and females from between 98 and 118 in (250–300 cm).

CONSERVATION STATUS
Currently listed as Data Deficient by the IUCN, even though it is not targeted specifically by the fishing industry. Listed mainly because of its capture as by-catch (which may be significant) and high-value fins.

SIGNIFICANCE TO HUMANS
The flesh is consumed commonly in the tropics and sold frozen, dried/salted, and smoked. Because of its large size, the great hammerhead was once believed to be dangerous. Attacks by hammerheads have occurred, but identifying the particular species is difficult; this species should be treated with caution. Important in the growing shark tourism industry, as it is observed by divers in many locations (e.g., in the Bahamas, Turks and Caicos, and Australia). ◆

Bonnethead shark
Sphyrna tiburo

FAMILY
Sphyrnidae

TAXONOMY
Squalus tiburo Linnaeus, 1758, "Habitat in America."

OTHER COMMON NAMES
French: Requin-marteau tiburo; Spanish: Cornuda tiburo.

PHYSICAL CHARACTERISTICS
Snout unique in being broadly rounded anteriorly (resembling a shovel) and without a median notch. Relatively tall first dorsal fin that is completely anterior to the pelvic fin origins; somewhat small second dorsal fin. Grayish-brown in color dorsally and on the sides and paler ventrally. Molariform posterior teeth. This is a small hammerhead species, reaching only about 5 ft (1.5 m) in length.

DISTRIBUTION
In the eastern Pacific from southern California south to Ecuador and in the western Atlantic, Caribbean, and Gulf of Mexico from North Carolina (exceptionally from New England) south to southern Brazil.

HABITAT
An inshore, coastal species, usually present in shallow waters down to depths of 82 ft (25 m) but occasionally down to 263 ft (80 m). Common in estuaries, sandy bottoms, coral reefs, shallow bays, and channels.

BEHAVIOR
Forms large schools in many regions of its range and is a social species, occurring typically in numbers from three to 15 individuals. Migrates seasonally and is found as far north as New England during the summer months. Sexual segregation has been noted in this species, with females remaining near shallow nursery areas to give birth. The behavior of this shark has been studied more intensely than that of others, and some 18 separate postures and behavioral patterns have been reported. Behaviors include patrolling (relatively straight-line swimming), maneuvering (systematic rapid turns), explosive gliding (rapid swimming initiated by tail beats), rapid head shaking, head snapping (strong vertical movements of the head and trunk), jaw snapping (opening and closing of the mouth), chafing (sudden rolling of the body), gill puffing (rapid expansion of the gills), clasper flexing (strong single clasper movements), circling head to tail (two sharks swimming in a tight circle, head to tail), and following (individuals closely following each other), among others.

FEEDING ECOLOGY AND DIET
Feeds abundantly on many different crustaceans (such as shrimp, isopods, crabs, lobsters, and even barnacles) as well as octopi, bivalves, and small fishes.

REPRODUCTIVE BIOLOGY
Viviparous with a yolk sac placenta and litters ranging from four to 16 young. Males are sexually mature at about 20.5–29.5 in (52–75 cm) in length and females by at least at 33 in (84 cm). Lengths at birth range from 13.4 to 15.7 in (34–40 cm).

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken frequently by small fishing operations, usually as bycatch in bottom trawls, and utilized fresh, frozen, dried/salted, and in other forms. Not considered dangerous, owing to its small size, but it occurs close to heavily populated areas and should be approached cautiously. ◆

Leopard shark
Triakis semifasciata

FAMILY
Triakidae

TAXONOMY
Triakis semifasciata Girard, 1854, San Francisco Bay, California.

OTHER COMMON NAMES
Spanish: Tollo leopardo.

PHYSICAL CHARACTERISTICS
The coloration of the leopard shark is distinctive, with numerous dark gray saddle marks from nape to tail, dark blotches laterally, and a light gray background color. First dorsal fin anterior to the pelvic fin origins and large second dorsal fin ahead of the anal fin origin. Slitlike eyes and upper and lower labial furrows. Reaches about 71 in (180 cm) in length.

DISTRIBUTION
Restricted to the eastern Pacific from Oregon to central Mexico, including the Gulf of California.

HABITAT
Occurs in shallow waters, usually less than 33 ft (10 m) deep, but may be captured as deep as 328 ft (100 m). A bottom dweller, the leopard shark commonly is found over rocky, sandy, or muddy substrates. Also may enter bays and estuaries.

BEHAVIOR
Leopard sharks are highly active, and the wide variety of prey items and their habitats indicate that they employ a wide range of feeding behaviors, from removing burrowing mollusks from their hard shells (clams) to feeding on schooling fishes. An abundant shark, with limited movements (as concluded by tagging studies), that is sometimes observed resting on the bottom.

FEEDING ECOLOGY AND DIET
Eats fishes and invertebrates; reported to prefer invertebrates, such as crabs, shrimp, polychaete worms, and octopi. Also reported to have fed on sharks (the brown smoothhound shark, *Mustelus henlei*), guitarfish (*Rhinobatos productus*), bat rays (*Myliobatis californica*), and fish eggs. Diet may vary according to size and season, at least locally off California. Feeds on many mud-burrowing prey items (clams, certain shrimps, and polychaetes), which suggests that feeding takes place close to the bottom. Feeding also has been observed closer to the surface, on schools of anchovies.

REPRODUCTIVE BIOLOGY
Aplacentally viviparous, with four to 29 young per litter. Gestation lasts about 12 months. Reproductive maturity may take more than 10 years, as growth is very slow.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, because of the lack of regulation with respect to fishing.

SIGNIFICANCE TO HUMANS
Leopard sharks are kept easily in aquaria, where they can live for more than 20 years. Seldom captured by anglers but caught somewhat more frequently by small commercial operations, especially in Mexico. The flesh is sold fresh or frozen and is reported to be of good quality. Not considered dangerous. ◆

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Marcelo Carvalho, PhD

Lamniformes
(Mackerel sharks)

Class Chondrichthyes
Order Lamniformes
Number of families 7

Photo: A basking shark (*Cetorhinus maximus*) feeding on plankton in the Irish Sea. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Living lamniform sharks are mere remnants of a much greater lamniform lineage that has, for the most part, become extinct. The 15 surviving species pale in comparison to the countless hundreds that have been described from fossil remains; the genus *Carcharodon* alone is known from some 10 fossil species, in contrast to the single extant *Carcharodon carcharias*. However, the overwhelming majority of these fossils consist of isolated teeth, first appearing in the fossil record during the early Cretaceous period some 120 million years ago (mya). Fossil lamniform teeth are known from many widespread marine localities from all continents, and they resemble those of living mackerel sharks in usually being slender, with very sharp cusps and arched roots. Many living lamniform species have closely related fossil relatives, again known only from teeth, going back at least to the Paleocene epoch (some 62 mya). Some of these fossil species are even placed in genera that are still extant (e.g., *Carcharodon*, *Odontaspis*), corroborating that lamniform sharks have a remarkably long evolutionary history, as do most living shark groups.

Fossil lamniforms known from more complete remains are extremely rare and include preserved partial skeletons of goblin sharks (Mitsukurinidae) from Lebanon (about 90 million years old), and vertebrae of various taxa, such as the megalodon shark from Europe (of Miocene to Pliocene age, some16 to 2.6 mya). The late Cretaceous goblin shark (*Scapanorhynchus lewisi*) is similar to the living goblin species (*Mitsukurina owstoni*) in having a very elongated snout, but it differs in having a much longer anal fin and more angular dorsal fins. Moreover, some features of its teeth and denticles differ as well. The megalodon shark (*Carcharodon megalodon*) is the most notorious fossil lamniform. It is known from huge, triangular teeth (as large as 7.9 in [20 cm] in height), that are very similar to teeth of the living white shark (*Carcharodon carcharias*). The megalodon shark, however, was much larger (estimated to reach up to 49 ft [15 m] in length), some three times the size of the living white, and was one of the greatest marine predators of all time (and the greatest macropredatory shark). Reconstructions of its jaws, believed to have been able to fit several people when agape, feature in many museum exhibits. Megalodon fossils are known from North and South America, the Caribbean, Europe, Australasia, Japan, and Africa.

Among living elasmobranchs (sharks and rays), lamniform sharks are more closely related to the ground sharks (Carcharhiniformes), bullhead sharks (Heterodontiformes), and carpet sharks (Orectolobiformes). These four orders, united in the larger group Galeomorphii, share various evolutionary innovations, such as the unique placement of the hyomandibula (a cartilage supporting the jaws posteriorly) on the skull. Within this group, lamniforms are most closely related to the ground sharks, as both orders share a tripodal rostrum supporting the snout internally.

Living lamniforms are among the most intensely studied and best-known sharks. Four of the living species were described in the eighteenth century, five in the nineteenth, and six in the twentieth century. (The last species described was the megamouth shark in 1983.) They are currently divided into seven families, 10 genera, and 15 species, and they were first recognized as a unique group by American ichthyologist David Starr Jordan (1851–1931) in 1923.

Phylogenetic (evolutionary) relationships among lamniform genera also have received much recent attention. The goblin shark (*Mitsukurina*) is considered the most basal, or primitive, living lamniform, followed by the sand tiger sharks (family Odontaspididae) and the crocodile shark (*Pseudocarcharias*). The remaining mackerel sharks have plesodic pectoral fin skeletons, in which the internal supports extend to the distal fin margin. Recent phylogenetic theories also support a common ancestry for a lamniform subgroup—comprising the basking shark and lamnids—with lunate caudal fins. Phylogenetic studies based exclusively on characters from the teeth disagree to some extent with those based on

A white shark (*Carcharodon carcharias*) approaches its prey from below where its gray topside camouflages its approach. (Photo by Corbis. Reproduced by permission.)

the skeleton, but teeth can often be misleading as indicators of evolutionary relationships in sharks and rays. Molecular phylogenies are also partly at odds with morphological ones, indicating that the evolutionary history of many lamniform genera is still in dispute.

Physical characteristics

Mackerel sharks are moderate to very large, ranging from about 3.3 ft (1 m) to 49 ft (15 m) in length. Some mackerel sharks, such as the great white and shortfin mako, are among the most popularly known and easily recognizable of all sharks. Other mackerel sharks are among the most bizarre and anatomically unique sharks, such as the megamouth, goblin, and thresher sharks. Lamniform sharks have unique teeth and intestines with a ring valve (with numerous, closely stacked turns).

There is some variation among lamniform species in relation to body and fin profiles, but all mackerel sharks have two dorsal fins (usually the first dorsal fin is very tall, while the second is reduced in height), large pectoral fins (except in the goblin and crocodile sharks, and to a lesser degree in the sand tiger sharks), and a small anal fin (except in the goblin and sand tiger sharks). The caudal fin is lunate or semilunate (i.e., with a well developed lower lobe) and upright in some species (basking shark and lamnids). Thresher sharks have caudal fins about equal to the length of the body, and goblin, sand tiger, megamouth, and crocodile sharks have caudal fins with relatively small lower lobes. The snout is conical in most species (except in the megamouth shark), and paddle shaped in the goblin shark; internally the snout is supported by a tripodal rostrum, usually composed of three cartilaginous segments. The spiracles are extremely reduced. The eyes are black and round in most species and lack nictitating (protective) membranes. Five pairs of gill openings are present. Denticles along the body are very small and do not form larger spines.

Some lamniform species, particularly those of the family Lamnidae (white, porbeagle, salmon, and mako sharks) are capable of maintaining slightly elevated body temperatures in relation to the surrounding water. This is accomplished in a manner similar to tunas and mackerels (bony fishes of the family Scombridae), through a counter-current, vascular heat-exchange system. The body musculature, viscera, brains, and eyes remain at temperatures from 5.4°F (3°C) to 25.2°F (14°C) warmer than ambient water. This physiological mechanism enables lamnid mackerel sharks to maintain higher metabolic rates; hence they are capable of great bursts of activity.

Lamniforms are usually blue or blue-gray on their dorsal and lateral sides, but white to off-white ventrally. Well-defined spots and blotches are mostly absent, but the white shark has black ventral pectoral fin extremities, and some species may have whitish blotches on the tail; the salmon shark, *Lamna ditropis*, has brown blotches on its lateral and ventral aspects.

Distribution

Mackerel sharks are found worldwide in tropical and temperate marine waters. Some species penetrate boreal and subantarctic seas (basking shark and species of the genus *Lamna*), and other species are extremely wide-ranging, such as the shortfin mako and white shark. All species are somewhat widespread.

Habitat

Mackerel sharks are present in shallow, coastal waters, as well as epipelagically and mesopelagically in deeper oceanic waters. Most species, such as the mako, white, and sand tiger sharks, occur predominantly in shallow areas, while others are demersal inhabitants of continental slope regions (e.g., the goblin shark).

Behavior

The behavior of sharks that inhabit oceanic realms is generally not well known. Lamniform sharks, however, display different behaviors in relation to feeding (from filter feeding to predation), as well as in relation to metabolism. The more

active species are laeterothermic (slightly warm-blooded); as a result they can swim at astounding speeds and are capable of great bursts of energy. The filter-feeding species, however, are relatively sluggish. Many species of lamniforms are known to leap completely out of the water (breaching), and not only as a result of being hooked on a line. The reasons behind this behavior are largely unknown but may have to do with escaping predators, snatching prey (as in the white shark), or ridding themselves of parasites. A lunate caudal fin may facilitate the strong upward swimming necessary to breach the water surface. Segregation by sex and size has been recorded in lamniform sharks, but much is yet to be learned about their population dynamics. More specific behavioral patterns have been described for particular species in the species accounts below.

Feeding ecology and diet

Almost all mackerel sharks are predaceous, extremely active eaters, feeding mostly on fishes belonging to numerous families (both bony fishes as well as sharks and rays), but also consuming large amounts of invertebrates (e.g., squids, octopi, gastropods, crustaceans) as well as marine mammals (pinnipeds, dolphins, and whales, as well as whale carcasses), marine turtles, and even oceanic birds. In contrast, two species, the megamouth and basking sharks, feed almost exclusively on zooplankton, and current evolutionary theories indicate that filter feeding evolved independently in both species, which also differ in their mode of filter feeding. Lamniform sharks are preyed upon by other shark species, including their own species.

Reproductive biology

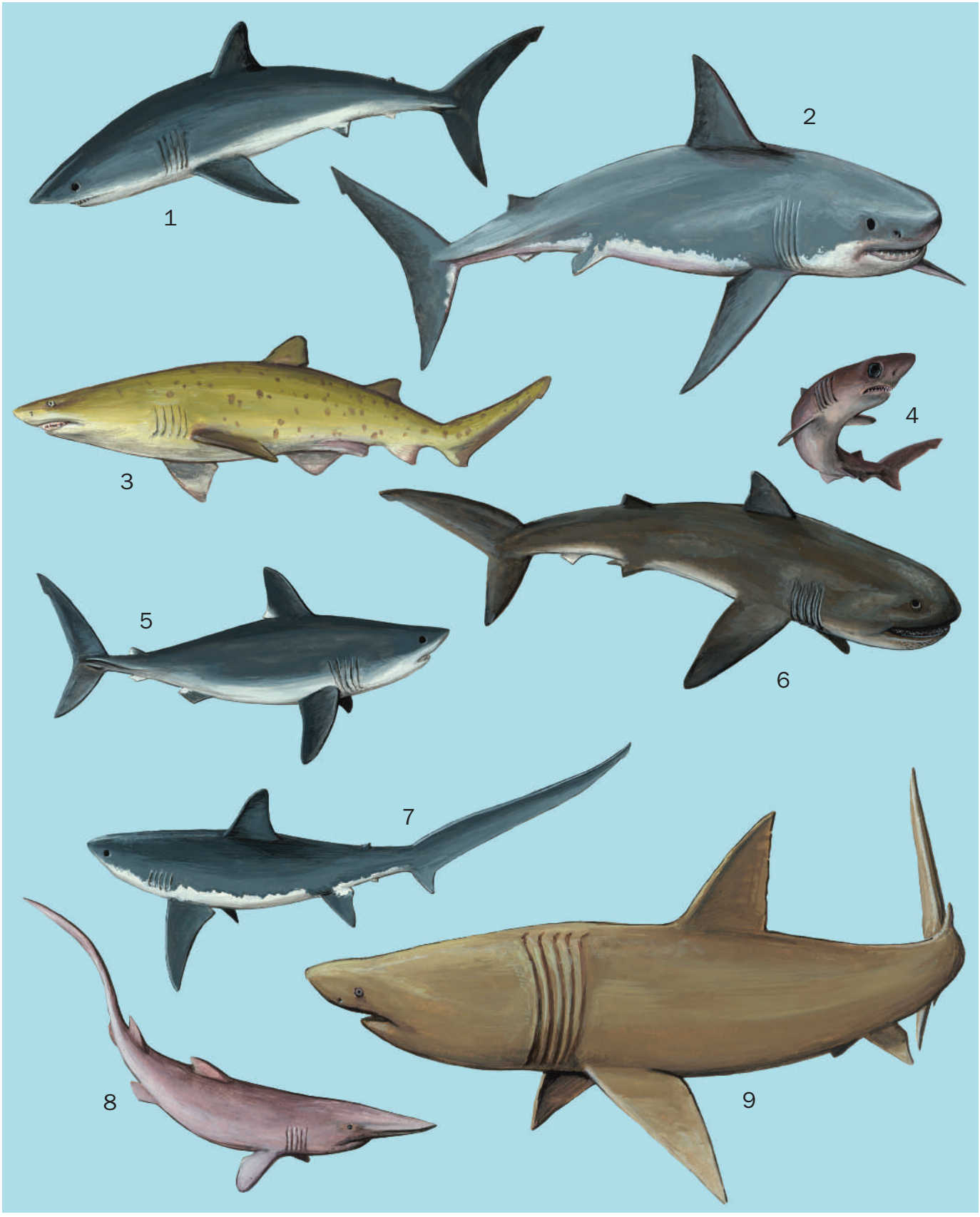
As far as is known, all species of mackerel sharks are yolk-sac viviparous (ovoviviparous, aplacentally viviparous); i.e., they give birth to live young that develop in utero and that feed on the yolk contents of their yolk sacs. But in many lamniform species, intrauterine cannibalism has been confirmed or is suspected. This occurs when embryos prey on each other (adelphophagy) or on other eggs (oophagy) inside the uterus after their yolk reserves are depleted. This group is the only elasmobranch taxon in which this occurs. Adelphophagy is known for certain in only one species, *Carcharias taurus*, but is suspected in others. Gestation periods vary among species and are comparatively poorly known. In some species, females are gravid from eight months to one year, while other species have longer gestations (up to 18 months). A period of reproductive inactivity may follow a gestation. Courtship patterns are presumably similar to those in many other sharks, with males biting females to subdue them prior to copulation and also during copulation.

Conservation status

The following species are listed by the IUCN: *Alopias vulpinus*, *Lamna ditropis*, *Megachasma pelagios*, and *Odontaspis noronhai* (as Data Deficient); *Carcharodon carcharias*, *Carcharias taurus*, and *Cetorhinus maximus* (as Vulnerable); *Lamna nasus*, *Isurus oxyrinchus*, and *Pseudocarcharias kamoharai* (as Lower Risk/Near Threatened).

Significance to humans

Many lamniform species are captured on longlines or trawls, either as bycatch or as specific targets, by the commercial fishing industry. The flesh is consumed fresh, frozen, smoked, or dried-salted, and their fins are procured by the destructive shark fin soup industry. Sport fishing for makos and other lamniforms is also common. This order contains what has been considered to be the most dangerous shark species, the white shark. But the misguided, anthropocentric perception that the white shark and other lamniform species are potential "man-eaters" has faded in the past decade; this negative image was given to this species mostly by sensationalistic media. Ironically, the roles are presently reversed, as it is now well understood that it is the sharks that are the victims of humankind, mostly through overfishing and the ruthless, cruel, shark fin soup fad, and not the other way around. In fact, many species of lamniforms and other sharks are quite valuable alive. The sand tiger shark is important as an exhibition fish in public aquaria, where it is relatively easily kept for long periods. Many lamniforms, such as the sand tiger, white, thresher, basking, and mako sharks, are even common ecotourist attractions in many places around the world.



1. Shortfin mako (*Isurus oxyrinchus*); 2.White shark (*Carcharodon carcharias*); 3. Sand tiger shark (*Carcharias taurus*); 4. Crocodile shark (*Pseudocarcharias kamoharai*); 5. Porbeagle (*Lamna nasus*); 6. Megamouth shark (*Megachasma pelagios*); 7. Thresher shark (*Alopias vulpinus*); 8. Goblin shark (*Mitsukurina owstoni*); 9. Basking shark (*Cetorhinus maximus*). (Illustration by Brian Cressman)

Species accounts

Thresher shark
Alopias vulpinus

FAMILY
Alopiidae

TAXONOMY
Squalus vulpinus Bonnaterre, 1788, Mediterranean Sea.

OTHER COMMON NAMES
French: Renard; Spanish: Zorro.

PHYSICAL CHARACTERISTICS
A very characteristic, large shark that may reach over 19.7 ft (6 m) in length, with an extremely elongated caudal fin (as long as the body), prominent first dorsal fin, minute second dorsal and anal fins, long pectoral fins, and small, conical snout. Coloration blue-gray to dark gray dorsally and laterally, with a white abdominal region, and white blotches laterally anterior to tail.

DISTRIBUTION
Circumglobal in both coastal and oceanic, tropical to temperate, waters.

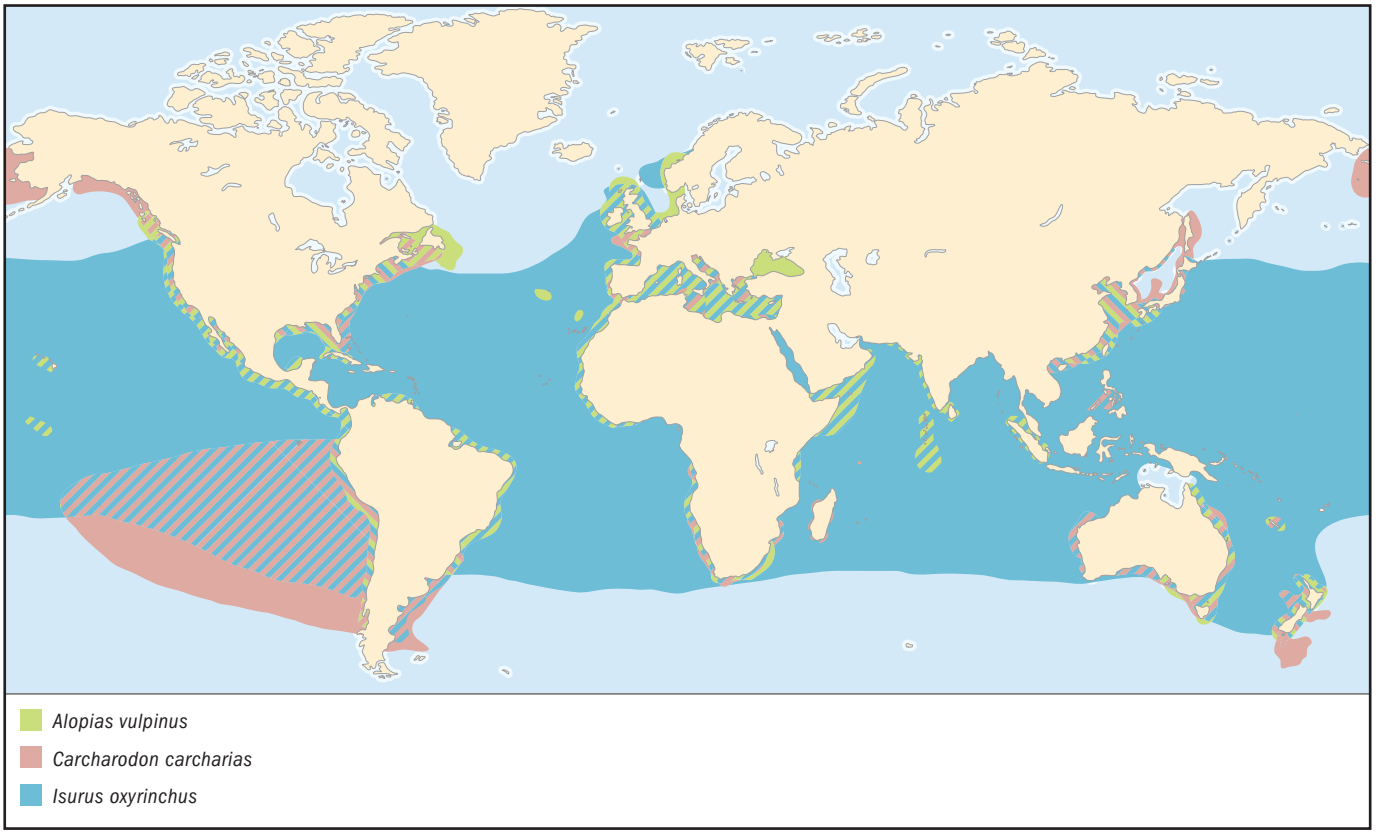
HABITAT
Usually occurs over the continental shelf region, close to the surface, but also occupying oceanic waters down to a depth of 1,200 ft (366 m). Younger specimens are more commonly found inshore.

BEHAVIOR
Thresher sharks are swift, vigorous swimmers, capable of breaching. They segregate by sex and migrate seasonally off the western coast of North America.

FEEDING ECOLOGY AND DIET
Preys mostly on a wide variety of epipelagic, midwater, and demersal fishes, but known to feed also on squid, octopi, pelagic crustaceans, and even seabirds. Uses its long tail to stun prey, entrapping them by swimming in increasingly smaller circles around schools of fishes, sometimes even in tandem with another thresher shark.

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, embryos apparently are uterine cannibals (oophagy). Litter numbers range from two to six, most commonly four; three to seven have been recorded in the eastern Atlantic. Young remain for a short period in shallow water nursing grounds. A gestation period of nine months has been reported for California populations, where mating occurs in the summer. Individuals are sexually mature between three and eight years old. Individuals may live for 50 years.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.



SIGNIFICANCE TO HUMANS
Caught by both commercial (mostly with longlines) and recreational fisheries, and consumed (or have been) in somewhat regular quantities in many locations, from almost all major oceans. Heavily fished off the West Coast of the United States in the late 1970s, but because overfishing led to a significant decline in stocks, the targeted fishery was terminated in 1990, though they were still captured as bycatch. Not considered dangerous, but they command respect because of their large size and possible aggressiveness. ◆

Basking shark
Cetorhinus maximus

FAMILY
Cetorhinidae

TAXONOMY
Squalus maximus Gunnerus, 1765, Norway.

OTHER COMMON NAMES
French: Pélerin; Spanish and Portuguese: Peregrino.

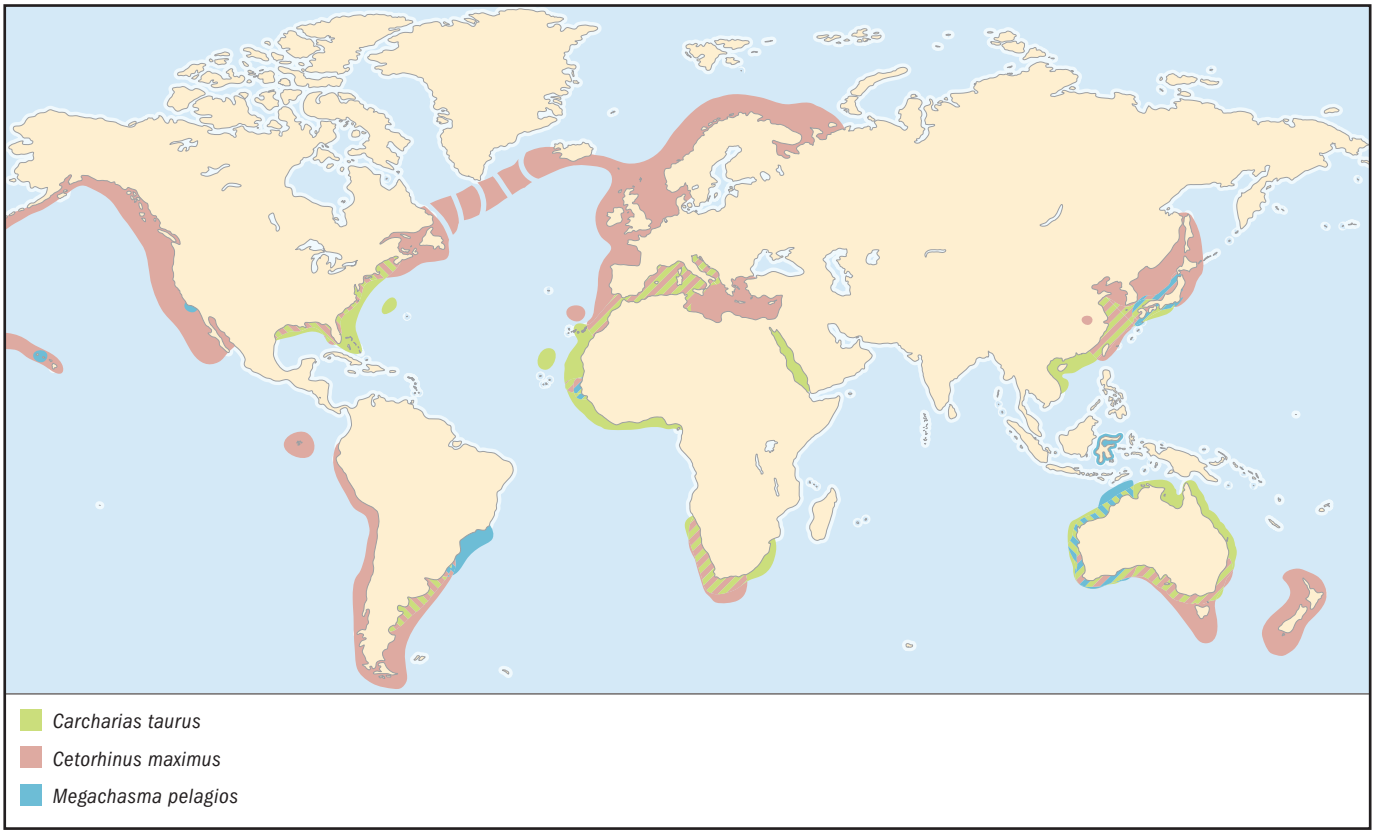
PHYSICAL CHARACTERISTICS
An unmistakable, huge shark, with extremely elongated gill slits (reaching from the dorsal to the ventral side), a very wide gill region when gills are expanded during feeding, a large, capacious mouth, well-developed gillrakers on the inside of the gills to capture small food particles, very small teeth, elongated pectoral fins, and a large lunate caudal fin. Grayish in color all around. Reported to reach 40–50 ft (12.2–15.2 m) in length, but large specimens are more common at about 33 ft (10 m).

DISTRIBUTION
Worldwide in mainly coastal, cold, temperate waters, most abundant off both sides of the northern Atlantic, but also in warmer, subtemperate regions such as the Mediterranean Sea.

HABITAT
Usually found over relatively shallow, coastal, pelagic waters but can be caught in open seas over deeper waters. Basking sharks appear in regular periods in certain areas (probably to feed) but also disappear in what appears to be regular cycles. Where they "disappear" to is a mystery, and perhaps they "hibernate" or spend periods of relative inactivity on or close to the bottom of the ocean.

BEHAVIOR
Basking sharks have been seen to leap clear out of the water (as have other mackerel sharks). Usually they are observed cruising at about 2.3 mph (2 knots) near or at the surface, with their mouths open during feeding. They are highly migratory, and several individuals may swim in tandem.

FEEDING ECOLOGY AND DIET
A filter-feeding shark, capable of taking in massive amounts of zooplankton. It swims with its mouth open very wide, retaining food items on its gillrakers, which are covered by denticles, giving them a rough texture. The gillrakers are shed periodically, usually in the early winter. Basking sharks feed mostly in the summer months near the surface. They either feed by alternative means when the gillrakers are shed, or remain without feeding, inactive, until they are regenerated. Food is retained in the gillrakers, aided by secretions of mucus in the pharynx, and subsequently swallowed when the mouth is closed.



REPRODUCTIVE BIOLOGY
Basking sharks employ yolk-sac viviparity, giving birth to two to six pups per gestation. The pups are the largest of all shark species, ranging 59–67 in (150–170 cm) in total length. Gestation periods are mostly unknown but are estimated to be very long (more than 1 year). The ovaries produce huge quantities of eggs.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN and protected in the United Kingdom, Malta, United States (East Coast), and New Zealand. Protection is pending in other areas (Mediterranean Sea, South Africa).

SIGNIFICANCE TO HUMANS
The basking shark has been captured in much of its range since the nineteenth century for its oily liver, which may contain up to 500 gal (1,893 l), meat (fresh and dried-salted), and skin, and also for its fins for the abhorrent shark fin–soup industry. Populations of the basking shark have declined significantly in many regions. The basking shark has some importance for the tourism trade, as it can be seen in many places, especially in the northern Atlantic (e.g., Bay of Fundy, Cape Cod, Isle of Man). Harmless, this shark poses no direct danger to people, but deserves respect because of its large size. ◆

White shark
Carcharodon carcharias

FAMILY
Lamnidae

TAXONOMY
Squalus carcharias Linnaeus, 1758, Europa.

OTHER COMMON NAMES
English: Great white shark; French: Grand requin blanc; Spanish: Jaquetón blanco.

PHYSICAL CHARACTERISTICS
Very large, reaching to 21.3 ft (6.5 m), more commonly to 18 ft (5.5 m), with a distinctive dentition comprised of large, triangular teeth with serrations on both edges, and with lateral cusps in embryos. They have a conspicuous white ventral coloration and a gray-to-bluish dorsal and lateral shade (the ventral and dorsal colorations are clearly separated on the sides), large gill slits, well-developed precaudal keels, a large first dorsal fin (much larger than the second), large and lunate caudal fin, pectoral fins with black tips ventrally, a conical snout, and a large, black eye.

DISTRIBUTION
Worldwide in coastal marine waters, and also around oceanic tropical islands, but more common in cold and warm temperate regions, and apparently rare or absent from most of the western Indian Ocean, Indonesia, and tropical Central America. Most common off California, Australia, and South Africa. Compared to other shark species, the white shark is relatively uncommon where it occurs.

HABITAT
The white shark is primarily a continental shelf inhabitant, cruising through relatively shallow waters either near the surface or close to the bottom. It also is found off oceanic islands and inshore bays and has even been captured on a bottom longline as far down as 4,199 ft (1,280 m). Capable of wide excursions in the pelagic realm.

BEHAVIOR
Whites are solitary and nomadic, and may occur in pairs, but feeding aggregations of some ten individuals also have been observed. It is known that they will leap completely out of the water (breaching) when capturing surface prey (or perhaps for other reasons). They are even capable of breaching vertically in a manner similar to dolphins. "Spy hopping" (when the shark will maintain its head out of the water as if to search the surroundings) and "repeated aerial gaping" (RAG; when the shark "bites" the air with its head clear out of the water) also have been observed. The white shark is known to satisfy its curiosity by circling intended prey items, or even boats and divers. It is capable of great bursts of speed. While feeding, their eyes roll back in their sockets. There may be segregation of individuals according to size.

FEEDING ECOLOGY AND DIET
The white shark is a formidable predator, feeding mainly on numerous families of bony fishes (as well as a large variety of sharks, even the basking shark), sea turtles, marine mammals (pinnipeds and whale carcasses), and even sea birds resting on the surface. Invertebrates also may be eaten (such as crabs), but most of its food comes from fishes and marine mammals taken from the surface or in the water column. White sharks are one of the top predators in the ocean; however, they sometimes fall prey to orcas (killer whales).

REPRODUCTIVE BIOLOGY
Embryos develop inside the uteri (yolk-sac viviparous), and intrauterine cannibalism (oophagy) is confirmed, as embryos have been found to have great amounts of yolk and egg membranes in their stomachs. Teeth also have been found in the stomachs of embryos, but embryos are believed to swallow their own teeth during development, as they undergo tooth replacement several times before birth. Gestation periods are mostly unknown. A litter of nine pups was reported for one pregnant female from the Mediterranean, and up to 10 embryos may reach term (data from gravid Japanese whites). The lack of knowledge concerning their reproduction is due to the scarcity of gravid females, perhaps an indication of pronounced segregation during gestation, or even of low fecundity. Size at maturity for females is between 13.1 ft (4 m) and 16.4 ft (5 m) long, and between 11.5 ft (3.5 m) and 13.1 ft (4 m) for males. Age at maturity ranges from 12 to 14 years for females and nine to 10 for males. Embryos measure 4 ft (1.2 m) to 5 ft (1.5 m) at birth, and can weigh up to 55 lb (25 kg). Courtship has been observed in one instance; the male bit the female into submission preceding a 40-minute-long copulatory embrace.

CONSERVATION STATUS
Presently threatened in many locations (e.g., Australia, South Africa) and heavily protected in Australia, South Africa, Namibia, Israel, Malta, and the United States. Australia is apparently the only country in which there is a detailed recovery plan for this species. Whites are listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
The white shark is perhaps the most notorious of all sharks, with an undeserved reputation as a "man-eater" and threat to humans. There are attacks on humans attributed to this species every year, but they average only about three per year from 1952 to 1992 (increasing slightly towards 1999). Attacks by the white are rare, however, when the whole phenomenon of

"shark attack" is taken into account. About 80% of all shark biting incidents have occurred in the tropics, where whites are far less common than in temperate zones. Attacks by whites are even more insignificant when one considers that more people have died from incidents with domestic livestock (e.g., pigs) than have died of attacks from this shark. Much of the maligned popular image is a result of the *Jaws* movies. However, it is the white shark that is in dire straits as a result of being slaughtered by recreational and commercial fishermen, either intentionally for trophies or as bycatch. Contrary to its folkloric, *Jaws* image, the white shark is worth more alive than dead and is an extremely valuable asset to ecotourism in many locations, attracting scores of interested onlookers who pay generously to see the creature from the protection of a submerged cage. Perhaps no other shark inspires as much fear and admiration as the white. A recent symposium volume (*Great White Sharks, The Biology of* Carcharodon carcharias) summarizes much valuable information concerning this species. ◆

Shortfin mako
Isurus oxyrinchus

FAMILY
Lamnidae

TAXONOMY
Isurus oxyrinchus Rafinesque, 1810, Sicily, Mediterranean Sea.

OTHER COMMON NAMES
French: Taupe bleu; Spanish: Marrajo dientuso.

PHYSICAL CHARACTERISTICS
A slender shark, with long, slightly curved teeth devoid of lateral cusps, slightly elongated pectoral fin, very lunate caudal fin with well developed lower lobe, conical snout, eyes not very large, very small second dorsal, pelvic, and anal fins. Reaches close to 13.1 ft (4 m) in length. Bluish dorsally and laterally, and white ventrally as well as on caudal fin.

DISTRIBUTION
Worldwide in tropical to temperate waters.

HABITAT
An oceanic and littoral shark, found from the surface down to 1,640 ft (500 m).

BEHAVIOR
The shortfin mako is probably the fastest and most agile of all sharks, jumping clear out of the water by several times its own length. Slightly endothermic, as its body musculature may reach up to 18° F (10° C) or more warmer than the temperature of the surrounding water. Highly migratory, capable of long-range migrations following warmer water masses.

FEEDING ECOLOGY AND DIET
Feeds mostly on fishes, both bony fishes as well as sharks and rays, squids, marine mammals, and turtles. Mako sharks are voracious feeders, consuming up to 3% of their body weight per day (compared to under 1% for many shark species), and digesting an average-sized meal in less than two days, whereas most sharks take some three to four days.

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, with uterine cannibalism (oophagy), and litters ranging from four to as many as 30 young (usually between 10 and 18). Gestation period long (possibly from 15 to 18 months). Size at birth ranging from 23 to 27 in (60 to 70 cm). Age of maturity may be from seven to eight years old.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Shortfin makos are fished significantly in many areas worldwide, recreationally, artisanally, and industrially. Because of their highly active demeanor and size, shortfin makos may be dangerous, even though there are few incidents recorded, most of which are accidents while fishing and handling live individuals. ◆

Porbeagle
Lamna nasus

FAMILY
Lamnidae

TAXONOMY
Squalus nasus Bonaterre, 1788, probably Cornwall, England.

OTHER COMMON NAMES
French: Requin-taupe commun; Spanish: Marrajo sardinero.

PHYSICAL CHARACTERISTICS
A somewhat stout shark, with a conical snout, large dark eyes, tips of pectoral fins slightly rounded, lunate caudal fin, teeth with small accessory cusps, bluish dorsal and lateral coloration (posterior tip of first dorsal white), and white ventrally. Reaches slightly over 9.8 ft (3 m) in length.

DISTRIBUTION
Occurs in warm, temperate, to cold waters in both the northern Atlantic, Mediterranean Sea, and in the Southern Hemisphere in the Atlantic and Indian Oceans, and off southern Australia.

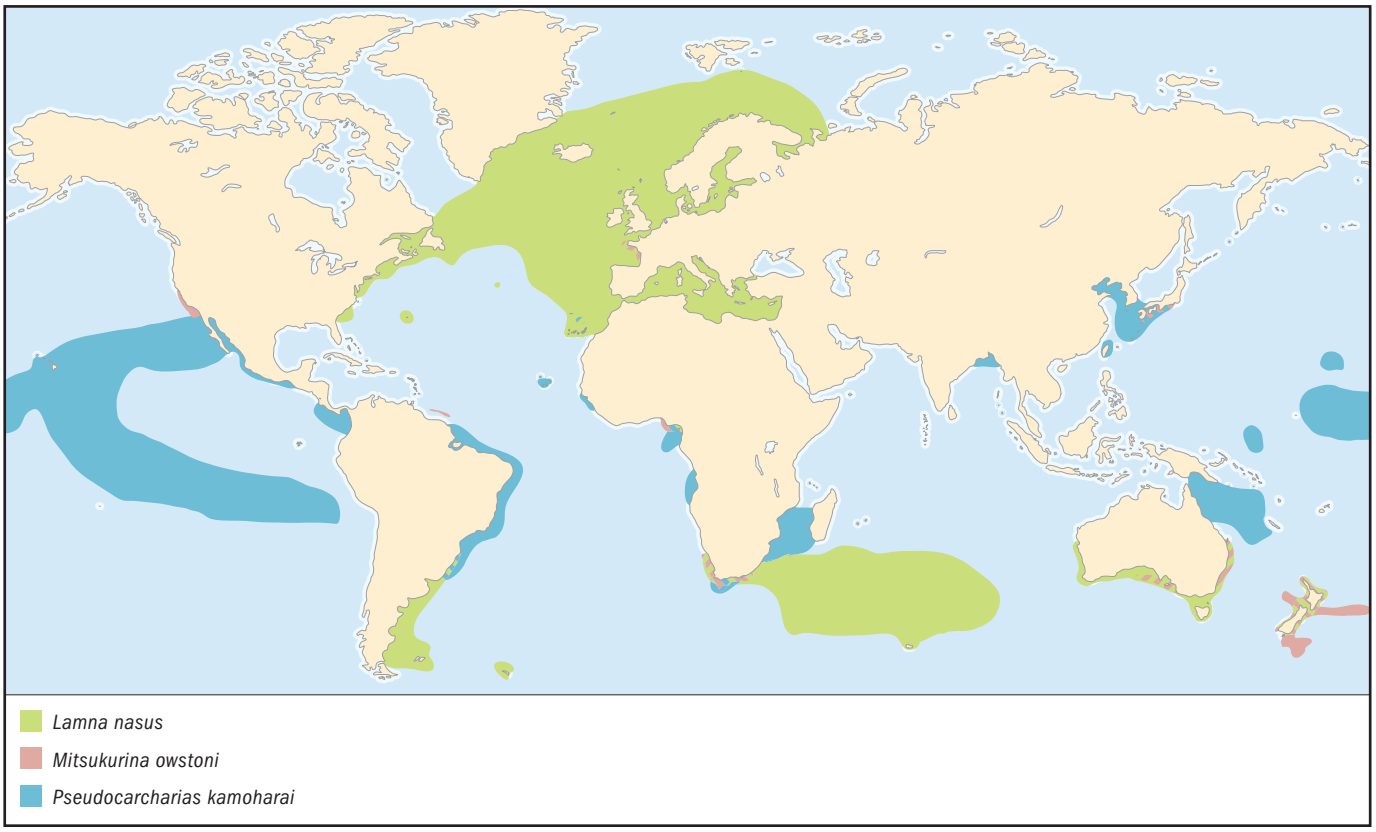
HABITAT
An epipelagic, littoral, and oceanic shark, most abundant on offshore fishing banks, usually in colder waters. Occurs from 3 to 2,296 ft (1 to 700 m) in depth.

BEHAVIOR
Porbeagles can be solitary or occur in schools. Usually migrates extensively at least in the northern Atlantic, and may aggregate by sex and size. An active, strong swimmer, capable of leaping out of water when captured.

FEEDING ECOLOGY AND DIET
Feeds mostly on fishes, both bony and cartilaginous, as well as on cephalopods. May be consumed by larger sharks.

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, with uterine cannibalism confirmed (oophagy). Litters vary from one to five young (usually four), and gestation periods are estimated to last between eight and nine months. Young inside uterus may have fang-like teeth specialized for tearing egg cases to release eggs for consumption. The fang-like teeth are then shed in utero. Young are born 23.6–29.5 in (60–75 cm) in length.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN.



SIGNIFICANCE TO HUMANS
Heavily fished for consumption, usually by longlining, but because of population declines, the porbeagle is now captured far less frequently. Overfishing is a concern especially in the North Atlantic, where the industry is regulated, but stocks may not be able to rebound. Recreationally fished as well, but individuals must be released upon capture. Not considered particularly dangerous to people. ◆

Megamouth shark
Megachasma pelagios

FAMILY
Megachasmidae

TAXONOMY
Megachasma pelagios Taylor, Compagno, and Struhsaker, 1983, Hawaii.

OTHER COMMON NAMES
French: Requin grand gueule; Spanish: Tiburón bocudo.

PHYSICAL CHARACTERISTICS
A remarkable, very large shark, up to 18 ft (5.5 m) long, with a very wide mouth, extremely elongated jaws that reach to the tip of the snout (the lower jaw is slightly longer than the upper jaw), endowed with minute teeth, a large head region, relatively small eyes, dense, papillated gillrakers, very long pectoral fins, low dorsal fins, and a large caudal fin. Coloration grayish blue dorsally and whitish ventrally.

DISTRIBUTION
Known from some 17 specimens from Japan, the Philippines, western Australia, California, southeastern Brazil, Senegal, and South Africa. Probably circumglobal in warm temperate to tropical waters.

HABITAT
A coastal and oceanic inhabitant, found in shallow waters some 16 ft (5 m) deep as well as in deep waters offshore, down to 545 ft (166 m) in waters up to 15,092 ft (4,600 m) deep. One specimen was stranded on a beach after washing ashore.

BEHAVIOR
A sluggish, solitary shark, capable of vertical migrations (perhaps following the movements of euphasiid shrimps). The megamouth shark is epipelagic but is capable of diving to great depths.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, especially euphasiid shrimp, copepods, and jellyfish, probably by taking in big gulps of water and retaining food on the very dense gillrakers. Luminous tissue lining the oral cavity may have a role in attracting prey items. Megamouths are the only known sharks with bite marks of the cookie-cutter shark (*Isistius brasiliensis*) and may be especially vulnerable because of their rather soft skin and slow-swimming behavior.

REPRODUCTIVE BIOLOGY
Mostly unknown, but probably yolk-sac viviparous, as are other lamniforms. Pregnant females have not been captured. Small oocytes, 0.2–0.4 in (5–10 mm) in diameter, were present in the ovaries of an adult female. Bite marks matching the teeth of

males also were present, and these have been interpreted as courtship scars.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
Caught occasionally as bycatch, but not consumed, though a Philippine specimen was apparently divided among fishermen. Of interest as a museum exhibit because of its extraordinary size and unusual features. The megamouth shark, only recently discovered, is one of the most spectacular ichthyological discoveries of the last 30 years and is the subject of a recent symposium volume, *Biology of the Megamouth Shark*, that provides much information on its anatomy and biology. ◆

Goblin shark
Mitsukurina owstoni

FAMILY
Mitsukurinidae

TAXONOMY
Mitsukurina owstoni Jordan, 1898, Japan.

OTHER COMMON NAMES
French: Requin lutin; Spanish: Tiburón duende.

PHYSICAL CHARACTERISTICS
A very unique shark, with soft, flabby flesh, an extremely elongated, paddle-shaped snout endowed with numerous pores of the ampullary sensory system, jaws that protrude greatly, very long, slender, sharp teeth without lateral cusps, a large anal fin, small dorsal fins, and long and low caudal fin. Captured specimens are off-white to pinkish white all over. Reaches some 12.5 ft (3.8 m) in length.

DISTRIBUTION
Scattered distribution on the continental slope, but probably worldwide.

HABITAT
A deep water, oceanic (found on seamounts), and continental slope shark, reaching depths of at least 4,265 ft (1,300 m).

BEHAVIOR
Mostly unknown, but a live specimen swam with its jaws tightly retracted, and not protruded as might have been expected.

FEEDING ECOLOGY AND DIET
Not well documented, but feeds on fishes and perhaps crustaceans.

REPRODUCTIVE BIOLOGY
Unknown, as no pregnant females have ever been recorded, but presumed to be yolk-sac viviparous, as are other lamniforms.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Taken on longlines, mostly as bycatch, but not fished significantly. Not considered dangerous because of its deep-water habitat. ◆

Sand tiger shark
Carcharias taurus

FAMILY
Odontaspididae

TAXONOMY
Carcharias taurus Rafinesque, 1810, Mediterranean Sea.

OTHER COMMON NAMES
English: Gray nurse shark (Australia); French: Requin taureau; Spanish: Toro bacota.

PHYSICAL CHARACTERISTICS
A relatively large shark, up to 9.8 ft (3 m) in length, with characteristic slender, sharp teeth (with lateral cusps), appearing to project outside of mouth (functional rows may point slightly forward), dorsal fins almost equal in size (first slightly larger), large anal fin, slightly rounded pectoral fin tips, conical snout, somewhat depressed head, clearly demarcated lateral line, and a light brown coloration, usually with slightly darker blotches scattered on body.

DISTRIBUTION
Distributed worldwide in tropical and warm temperate waters, but absent at least from the eastern Pacific, and probably also from the Caribbean and eastern North Atlantic (north of Africa).

HABITAT
Mostly an inshore species, found in shallow waters, but recorded to occur down to 627 ft (191 m), and may occur either close to the bottom, at the surface, or midwater.

BEHAVIOR
Mostly nocturnal and solitary, but may form large schools, and capable of extensive migrations. Individuals aggregate for courtship, mating, feeding, and birth, and the sand tiger is capable of social interactions. Behavior in this species is known from aquarium observations, indicating that sand tiger sharks display specific patterns related to courtship and mating. These include specific movements of the claspers in males, submissive behavior by females, males poking the cloaca region of females with their snouts, and males biting females to establish dominance, among other behaviors. Sand tiger sharks will periodically gulp air into their stomachs from the surface, apparently as a buoyancy control.

FEEDING ECOLOGY AND DIET
Sand tiger sharks feed mostly on a wide range of fishes, including many families of pelagic and demersal bony fishes, as well as sharks and rays, cephalopods, crustaceans, and marine mammals.

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, with embryos consuming other embryos (adelphophagy) and eggs in uteri. Gestation varies from 9 to twelve months. Two young are born in a litter, one per uterus, but a cluster of 16 to 23 eggs are grouped together in egg cases within each uterus after fertilization. From this group, only one embryo will be dominant, feeding on other embryos and eggs and even moving vigorously within the uterus. Young are born at about 3.3 ft (1 m) in length, but already have sharp teeth at 6.7 in (17 cm). Breeds every other year.

CONSERVATION STATUS
Protected in Australian waters since 1984 because of steady declines in its populations as a result of overfishing, and listed as

Vulnerable by the IUCN. Local protection measures are in place in many regions, including the eastern coast of the United States since 1997.

SIGNIFICANCE TO HUMANS
Commonly displayed in aquaria, where specimens can live for extended periods, surpassing 30 years. Not considered particularly dangerous, but because it appears ferocious, sand tigers have been implicated in attacks off Australia that are probably the result of other shark species. Observations conducted in the wild and in aquaria indicate that this species is harmless and presents no real danger to divers. Important to the ecotourism industry, as many trips feature observations of wild sand tiger sharks. ◆

Crocodile shark

Pseudocarcharias kamoharai

FAMILY
Pseudocarchariidae

TAXONOMY
Carcharias kamoharai Matsubara, 1936, Japan.

OTHER COMMON NAMES
French: Requin crocodile; Spanish: Tiburón crocodilo.

PHYSICAL CHARACTERISTICS
A slender, relatively small shark up to 43 in (110 cm) in total length), with very large, blackish eyes, long, pointed teeth with minute lateral cusps only on lateral tooth rows (fewer than 30 total tooth rows in either jaw), pointed snout, low dorsal fins, and rounded pectoral fin tips.

DISTRIBUTION
Worldwide in tropical marine waters, but with a scattered distribution, needing confirmation from many areas.

HABITAT
Inhabits the tropical pelagic realm, but can occasionally be captured closer to shore. Reaches 984 ft (300 m) in depth.

BEHAVIOR
Mostly unknown, but is believed to be a fast-swimming shark, probably capable of leaping out of the water. Its large eyes might indicate either nocturnal activity or feeding at great depths.

FEEDING ECOLOGY AND DIET
Feeds mainly on pelagic or mesopelagic fishes (e.g., bristlemouths [Gonostomatidae], lanternfishes [Myctophidae]), and invertebrates such as squids.

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, giving birth to four pups at a time (two per uterus). Uterine cannibalism has been recorded, with more developed fetuses eating remaining eggs, and, uniquely, two individuals surviving per uterus. Gestation periods mostly unknown.

CONSERVATION STATUS
Considered at Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Fished by longlines off Japan, but not significantly consumed. Because of its pelagic nature, there is little interaction with people, and hence the species is not considered dangerous.

Resources

Books

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American Elasmobranch Society, Florida Museum of Natural History. Gainesville, FL 32611 USA. Web site: <http://www.flmnh.ufl.edu/fish/Organizations/aes/aes.htm>

Marcelo Carvalho, PhD

Hexanchiformes
(Six- and sevengill sharks)

Class Chondrichthyes
Order Hexanchiformes
Number of families 2

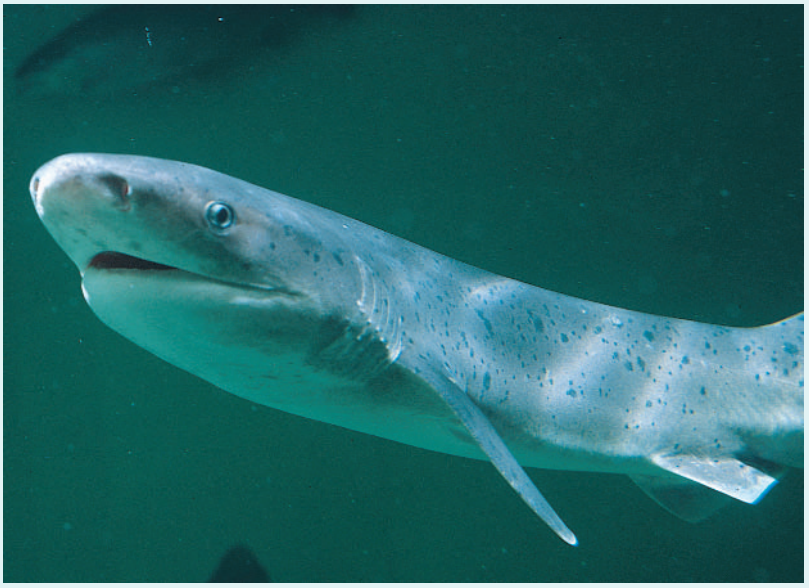


Photo: The broadnose sevengill sharks (*Notorynchus cepedianus*) bear the most resemblence to prehistoric sharks and, therefore, are considered to be more primitive than the sharks with five or six gills. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Hexanchiforms are an ancient lineage, as well-documented fossil skeletons of *Notidanoides muensteri* date from the late Jurassic (some 150 million years ago, or mya) Solnhofen limestones of southern Germany. *Notidanoides* was a large shark, up to 9.8 ft (3 m) in length, with features suggestive of modern hexanchiforms, such as a single dorsal fin. Its teeth, with multiple cusps arranged in a series, indicate that it is related closely to the Hexanchidae. Most fossil hexanchiforms are known from isolated teeth found in all continents, ranging from the early Jurassic (180 mya) to the Tertiary, which makes the order one of the longest-surviving shark lineages. Many late Cretaceous to Tertiary species are even assigned to living genera, based on fossil teeth. The hexanchiform fossil record indicates that they were never very diverse, but more so than at present, as there are only five living species.

The bizarre frilled shark (*Chlamydoselachus anguineus*) was first described by the American zoologist and chondrichthyan taxonomist Samuel W. Garman in 1884. It has teeth that resemble those of some Paleozoic sharks ("cladodont teeth"), which led many early researchers to consider it a relic of Devonian seas. It is now well established, however, that *Chlamydoselachus* shares a more recent common ancestry with all living sharks and rays (the Neoselachii), only distantly related to Paleozoic forms.

Sixgill and sevengill sharks are the most basal ("primitive") members of the large group known as the Squalea, which includes the dogfishes and allies (Squaliformes), the angelsharks (Squatiniformes), the sawsharks (Pristiophoriformes), and the rays, or batoids (Batoidea). The Squalea group is characterized by numerous evolutionary specializations, such as complete hemal arches (ventral projections arising from the vertebral column) in the trunk region anterior to the tail. There has been debate as to whether the frilled shark is actually part of the Hexanchiformes or rather belongs in an order of its own, but derived features shared with other hexanchiforms support its placement within the order (e.g., the extra gill arch and more heart valve rows).

The five extant species of hexanchiforms are divided into two families: Chlamydoselachidae (*Chlamydoselachus anguineus*) and Hexanchidae (*Hexanchus griseus*, *H. nakamurai*, *Notorynchus cepedianus*, and *Heptranchias perlo*). The latter family also is known as "cowsharks."

Physical characteristics

The hexanchiform families are very distinct in their morphological characteristics. *Chlamydoselachus* is a highly modified and unique shark, with an eel-like body, an enlarged mouth, and well-delimited rows of teeth. (Its teeth are unlike those of any other living shark.) It shares with hexanchids a single, posteriorly located dorsal fin and a long caudal fin, an extra gill arch (hexanchiforms have either six or seven gill arches and gill slits on each side), small spiracles, a clearly demarcated lateral line along the trunk and precaudal tail regions, and a mouth extending posteriorly behind the level of the eyes. Hexanchids have unique teeth that are highly differentiated between the upper and lower jaws and also along either jaw. The upper jaw teeth are small and flattened, with either a single cusp or very small accessory cusps; the lower jaw teeth are very wide and flattened, with multiple prominent cusps in addition to a median (symphysial) tooth and smaller, blunt posterior teeth. Hexanchiforms are

noteworthy for having mostly uncalcified vertebrae and notochords with little constriction.

Chlamydoselachus is a uniform dark brown to grayish brown in color, whereas hexanchids are mostly gray without strong color patterns. The exception is *Notorynchus*, which has darker spots. *Notorynchus* and *Hexanchus griseus* attain very large sizes, but the remaining species are more moderate in size, usually not surpassing 63 in (160 cm) in length.

Distribution

These fishes are found worldwide in tropical and temperate waters, but most species have a spotty distribution, that is, they are known from many isolated regions without records from intermediate areas. Because most hexanchiform sharks occur along the continental slopes, their scattered distribution may be only an artifact of sampling.

Habitat

Most species are deepwater inhabitants, occurring demersally along the continental slopes but sometimes venturing into more shallow pelagic or inshore waters. The primary exception is *Notorynchus cepedianus*, which also is a coastal species. There are shallow-water records for *Heptranchias perlo* and *Hexanchus griseus* as well, but these species are more common in waters deeper than 328 ft (100 m). Some species also have been recorded from oceanic islands.

Behavior

Little is known concerning their behavior, but individuals of *Notorynchus cepedianus* may hunt cooperatively. Sharks are almost exclusively solitary hunters, but broadnose sevengills have been observed hunting as a pack off the coast of Namibia. Individuals circled a large fur seal (which can weigh 770 lb, or 350 kg, more than the shark) and slowly closed in by tightening the circle. After one shark initiated an attack, the remaining sharks followed suit. Hexanchiforms may migrate vertically, entering more shallow waters at night. Some species migrate vertically in the water column, remaining closer to the bottom during the day and ascending to the surface to feed at night.

Feeding ecology and diet

Sixgill and sevengill sharks feed on a variety of bony fishes, sharks, and rays as well as invertebrates. Marine mammals (seals and dolphins) also are consumed. Bony fishes include numerous benthic and demersal families, but pelagic species also are eaten. Some hexanchiform species are known to have attacked individuals of the same species that have been hooked, biting off pieces while they were being reeled or towed in. Because of their mostly obscure habitats, very little is recorded concerning their feeding ecology. At least one species may hunt in packs. Hexanchiform sharks are presumably consumed by larger sharks, including of their own species, but little data exist in relation to their predators.

Reproductive biology

All species are ovoviviparous (aplacentally viviparous), and the young derive their nourishment exclusively from the yolk sac before birth. Litters can be very large in the two largest species. (More than 100 pups may be born at once in the case of the bluntnose sixgill shark.). Only up to 20 (usually about 12) young are present per litter, however, in the three remaining species (sharpnose sevengill shark, *Heptranchias perlo*; the bigeyed sixgill shark, *Hexanchus vitulus*; and the frilled shark, *Chlamydoselachus anguineus*). Females of the two largest species give birth to young in shallow-water nurseries (though not exclusively for the bluntnose sixgill shark, which also gives birth in other locations). Lengths at birth range from 10.2 to 25.6 in (26–65 cm). Almost nothing is known concerning gestation periods and other details of reproductive biology.

Conservation status

Two of the five currently recognized species of hexanchiforms are listed by the IUCN. *Hexanchus griseus* is considered Lower Risk/Near Threatened, and *Notorynchus cepedianus* is cited as Data Deficient.

Significance to humans

Certain hexanchiform species are fished commercially but not to a significant extent. They may be used fresh, frozen, or dried/salted, and the flesh of at least one species (*Notorynchus cepedianus*) is said to be of good quality. The skin of these sharks is used as leather (particularly in China). Hexanchiforms are not considered to be strictly dangerous, but because of the large sizes of at least some species, they should be approached with caution; very few attacks are attributed to sharks of this order. They are not hardy aquarium sharks. Two species (*Notorynchus cepedianus* and *Hexanchus griseus*) have been seen in the wild by tourists. The former species is seen in many areas of its shallow-water range (e.g., in Humboldt Bay and San Francisco Bay, California, United States). The latter was sighted through commercial operations that (until recently) took tourists out in small submersibles to see young sharks at depths of about 656 ft (200 m) off Hornby Island, British Columbia. Diving to observe *Hexanchus griseus* in the Strait of Georgia (between British Columbia, Canada, and the United States) also is possible during the summer months, at depths from 79 to 138 ft (24–42 m).

1. Frilled shark (*Chlamydoselachus anguineus*); 2. Bluntnose sixgill shark (*Hexanchus griseus*); 3. Broadnose sevengill shark (*Notorynchus cepedianus*). (Illustration by Brian Cressman)

Species accounts

Frilled shark
Chlamydoselachus anguineus

FAMILY
Chlamydoselachidae

TAXONOMY
Chlamydoselachus anguineus Garman, 1884, Japan.

OTHER COMMON NAMES
French: Requin lézard; Spanish: Tiburón anguila.

PHYSICAL CHARACTERISTICS
A slender, eel-like shark, with a single, low dorsal fin close to the caudal fin; long pelvic, anal, and caudal fins; six gill arches; very elongated gill slits reaching from the dorsal to the ventral side (the first gill slit is especially elongated); a huge mouth with clearly separated rows of numerous teeth (approximately 300), and ventral keels along trunk and tail. The teeth are similar in the upper and lower jaws; there are three long and very sharp, slender cusps with two minute cusplets between. Coloration is a uniform dark brown. Reaches perhaps 77.6 in (197 cm) in length, but more common at about 55 in (140 cm).

DISTRIBUTION
Known from many localities scattered in all major oceans but absent from the Mediterranean Sea.

HABITAT
A primarily deepwater species, demersal on the outer continental shelf and slope at depths from about 394 to 4,265 ft (120–1,300 m) but occasionally caught at the surface.

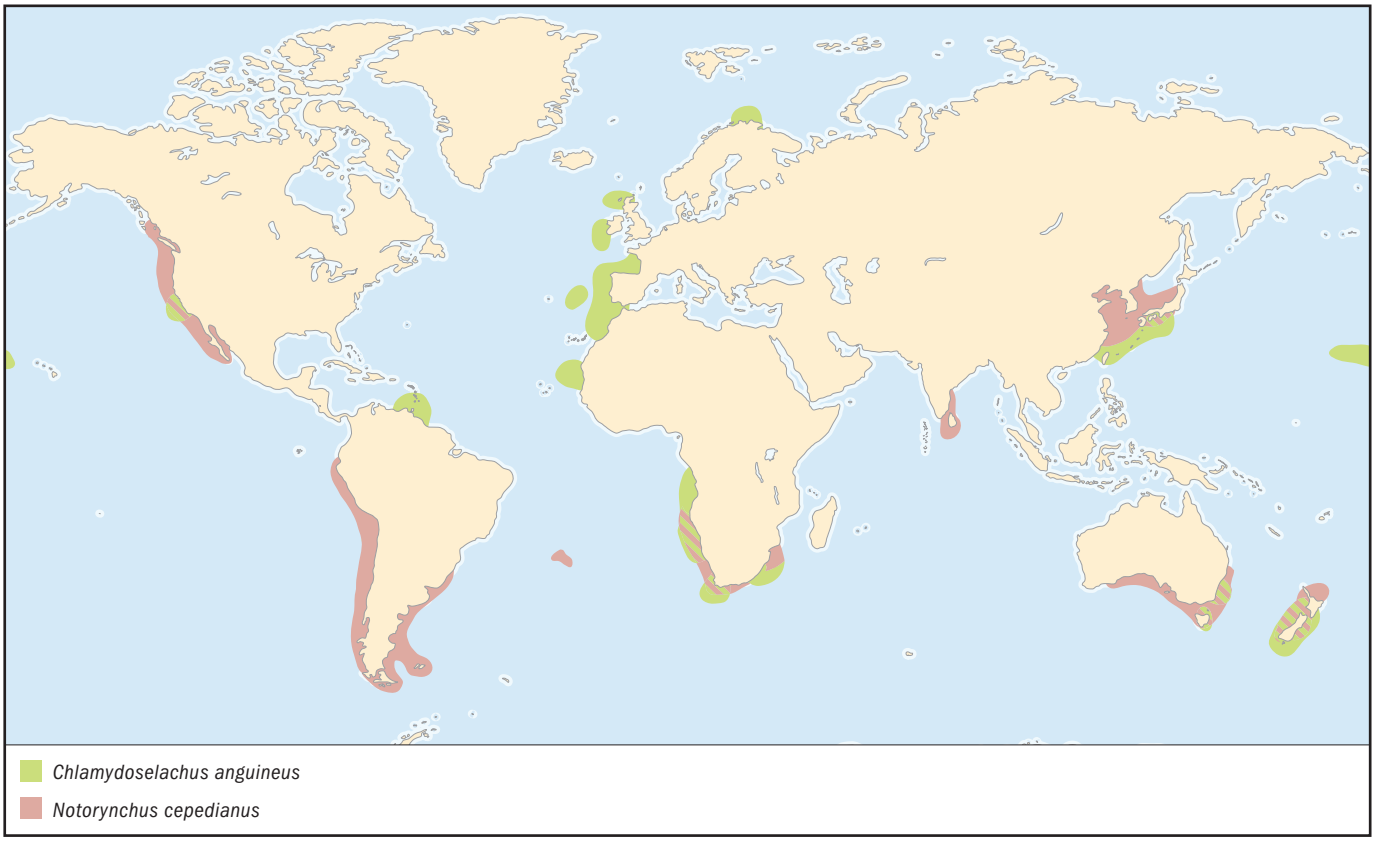
BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Mostly unknown, but its teeth suggest that it feeds on deepwater demersal and benthic fishes and cephalopods or other soft invertebrates. The huge gape of its mouth indicates that this species is capable of swallowing large prey items. Predators of the frilled shark are unknown.

REPRODUCTIVE BIOLOGY
Ovoviviparous (yolk sac viviparous), with litters ranging from eight to 12 young. Reproduces year-round off Japan. Gestation periods are not known but are estimated at between 1 and 2 years. Size at birth is about 15.7 in (40 cm); sexual maturity for males is reached at about 39.4 in (100 cm) and for females at about 53 in (135 cm). Breeds from March to June (in Japan).

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken incidentally as bycatch by trawls or bottom longlines; not considered a significant food item but may be utilized for



fishmeal and human consumption. The remarkable appearance of this shark gives it a menacing and ferocious aspect, but because of its depth distribution, it is not considered dangerous. Unquestionably one of the most bizarre sharks known. ◆

Bluntnose sixgill shark

Hexanchus griseus

FAMILY
Hexanchidae

TAXONOMY
Squalus griseus Bonnaterre, 1788, Mediterranean Sea.

OTHER COMMON NAMES
French: Requin grisé; Spanish: Cañabota gris.

PHYSICAL CHARACTERISTICS
A stout-bodied, large shark that may reach 16.4 ft (5 m) in length, with a broad, blunt snout; relatively small eyes; six pairs of gill slits; a large caudal fin; a single dorsal fin situated close to the caudal fin, and broad and flattened teeth. There are eight to 10 posteriorly directed cusplets per tooth in the first six teeth of the lower jaw (except the symphysial tooth), and the upper teeth usually have a single cusp. Coloration is a uniform gray to dark brown.

DISTRIBUTION
Worldwide in temperate and tropical seas, including the Mediterranean Sea.

HABITAT
This species may be demersal along the continental slopes down to some 6,151 ft (1,875 m), but it also may occur pelagically at the surface. Young individuals are more common inshore, while larger adults are more common in deeper waters.

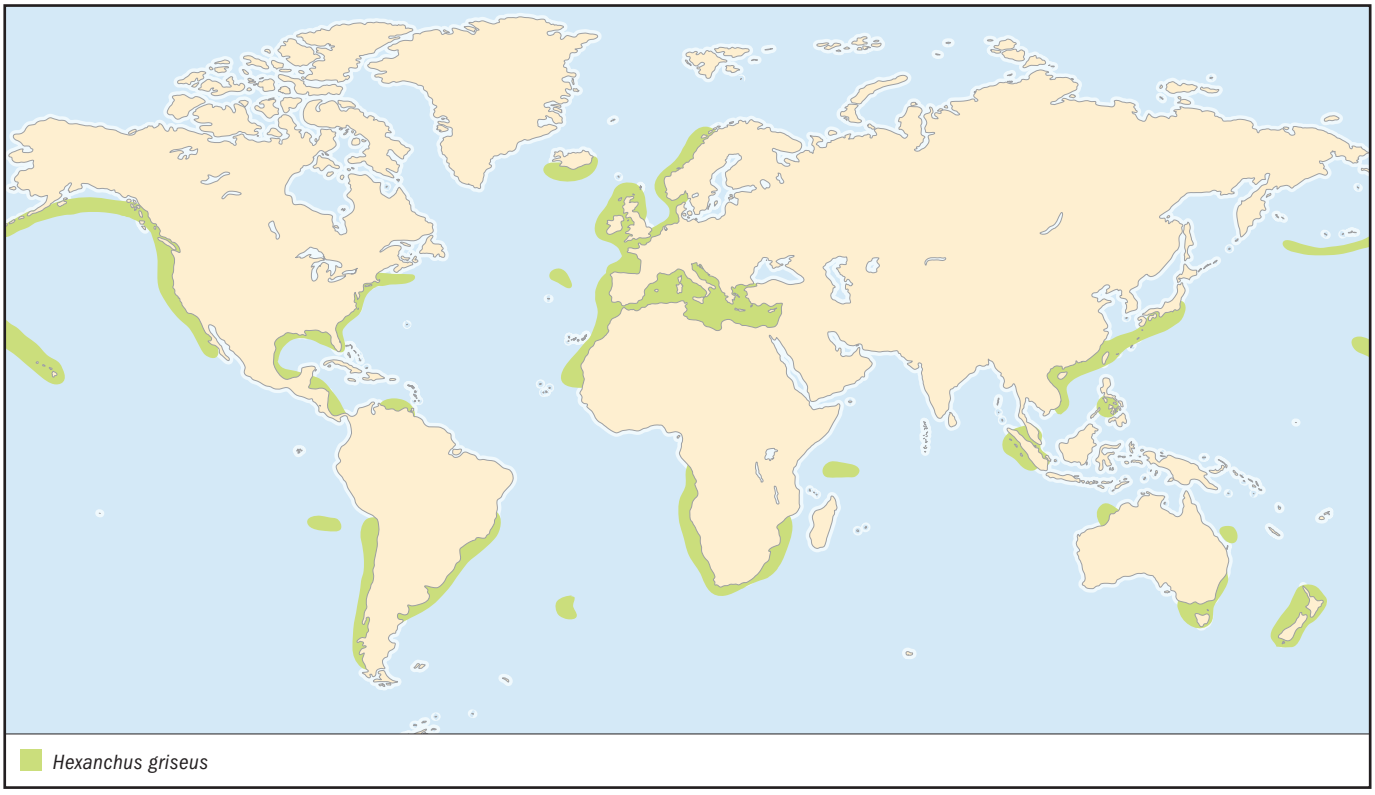
BEHAVIOR
A solitary, sluggish shark but also capable of strong swimming. Apparently sensitive to light. May migrate vertically to feed at night.

FEEDING ECOLOGY AND DIET
Feeds on a wide range of fishes, including swordfishes, marlins, dolfinfishes, herrings, grenadiers, cod, hake, ling, and flounders as well as sharks (including hooked individuals of its own species) and rays. Also eats invertebrates (squids, crabs, shrimps) and seals. Predators are unknown for this species, although presumably it may be eaten by larger sharks (including those of the same species).

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, with large litters that range from 22 to 108 young. Gestation periods are unknown. Gravid females may give birth in shallow bays. Size at birth is about 25.6 in (65 cm). Females are sexually mature at about 177 in (450 cm) and males at slightly smaller sizes.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN. As *Hexanchus griseus* is fished for both food and sport and also taken as bycatch, it may not be able to sustain target fisheries. Regional populations are already depleted (e.g., in the northeast Pacific), but fisheries data are generally lacking. Efforts to protect this species are not yet under way.

SIGNIFICANCE TO HUMANS
Not considered a dangerous species, but because of its size, it should be approached with caution. Young individuals are known to thrash about violently when captured. It is not



consumed much, but it is captured in pelagic and bottom trawls and by line and utilized locally for meat, oil, and fishmeal. Can be seen during the summer months off Hornby Island and also Vancouver Island (British Columbia), as young individuals penetrate into the shallow waters of the Strait of Georgia (located between British Columbia, Canada and the United States). They are observed more readily at night. ◆

Broadnose sevengill shark

Notorynchus cepedianus

FAMILY
Hexanchidae

TAXONOMY
Squalus cepedianus Peron, 1807, Tasmania, Australia.

OTHER COMMON NAMES
French: Platnez; Spanish: Cañabota gata.

PHYSICAL CHARACTERISTICS
A large shark, reaching at least 9.8 ft (3 m) in length, possibly 13 ft (4 m), with a broad head; seven pairs of gill slits; a moderately tall, single dorsal fin; and large pectoral and caudal fins. The first six pairs of teeth of the lower jaw are wide and flattened, with four to five posteriorly pointed cusps (except the symphysial tooth); the upper teeth usually have single cusp. Background coloration is gray to brown but mottled with numerous, small darker spots and blotches.

DISTRIBUTION
Widely distributed in temperate seas (unknown in the Indian Ocean and Mediterranean Sea) and more abundant in the Pacific Ocean. Common off the coasts of South Africa and Namibia.

HABITAT
A coastal species reaching depths of only some 443 ft (135 m) on the continental shelf and frequently found in very shallow water, bays, and close to shore.

BEHAVIOR
Considered to be an active, powerful shark that usually is observed cruising slowly near the surface but is capable of quick bursts of speed. May be aggressive if provoked and is known to snap vigorously when captured. Speculated to coordinate its entry into shallow bays with tidal fluxes. Cooperative hunting ("social facilitation") has been recorded for this species in addition to three other predatory strategies (stealth, ambush, and bursts of speed). Spy-hopping, in which an individual raises its head out of the water in a vertical position (possibly to see the surroundings), also has been recorded.

FEEDING ECOLOGY AND DIET
Feeds voraciously on many different families of fishes (including salmon, anchovies, and sturgeon) and also on sharks (dogfishes, houndsharks, and hooked individuals of its own species) and rays (such as eagle rays). Predators are unknown for this species, although presumably it may be eaten by larger sharks (including those of the same species).

REPRODUCTIVE BIOLOGY
Yolk-sac viviparous, with large litters of up to 82 young. Gravid females give birth in shallow bays during the warmer months. Gestation periods are unknown. Size at birth is between 17.7 and 20.9 in (45–53 cm). Males are sexually mature at 59–71 in (150–180 cm) and females at larger than 78.7 in (200 cm). One instance of copulation was observed at around noon in the shallow waters of Namibia, in which it was clear that the male held the female with his mouth. The eggs are relatively large, measuring some 3 in (7.5 cm) in diameter.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
Fished for its high-quality flesh in many areas where it occurs. Also fished for sport (in the United States, Australia, and South Africa) and for its skin (in China) for the production of leather. Owing to its large size and putative aggressive behavior, this shark should be approached cautiously. It has been implicated in several attacks on people (in California and South Africa), but these attacks may have been by other species. It is known to have attacked divers while in captivity. ◆

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Marcelo Carvalho, PhD

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Squaliformes
(Dogfish sharks)

Class Chondrichthyes
Order Squaliformes
Number of families 7

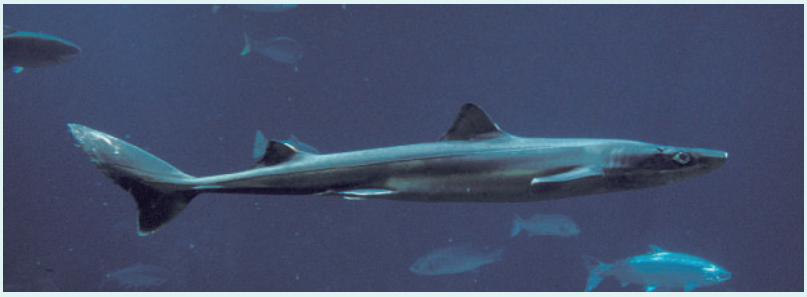


Photo: The piked dogfish (*Squalus acanthias*) is the world's most abundant shark. (Photo by Monterey Bay Aquarium Foundation. Reproduced by permission.)

Evolution and systematics

The order Squaliformes contains 22 genera, 98 formally described species, and at least 17 known but undescribed species. However, higher-level systematics is not pure science, and hence it should not be surprising that experts may define the order Squaliformes somewhat differently. Some do not include the bramble sharks, Echinorhinidae, and others exclude additional groups, justifying their decisions on various fine morphological details. In this chapter, we will consider the order Squaliformes to comprise a more traditional and inclusive group of sharks, which includes the bramble sharks (Echinorhinidae), the dogfish sharks (Squalidae), the gulper sharks (Centrophoridae), the lantern sharks (Etmopteridae), the sleeper sharks (Somniosidae), the rough sharks (Oxynotidae), and the kitefin sharks (Dalatiidae). Fossils interpreted as representing Squaliformes have been laid down in deposits at least 150 million years old, and future discoveries will surely push this trail marker back deeper into the past. Amongst living elasmobranches, Squaliformes is usually accepted as a sister group to an evolutionary branch consisting of angel sharks (Squatiniformes), saw sharks (Pristiophoriformes), and rays. Defining membership within Squaliformes based on an unshared morphological character is not possible, and thus crafting a membership card for this order of fishes may have to await the results of molecular studies.

Physical characteristics

Squaliformes includes fishes that rank as the smallest and amongst the largest of all living sharks, from spined pygmy sharks (*Squaliolus*) growing only to about 10 in (25.4 cm) long, to Greenland sharks (*Somniosus microcephalus*) and Pacific sleeper sharks (*S. pacificus*) estimated at over 20 ft (6.1 m) long. These sharks are a mixed lot; however, and a general diagnosis of their physical characteristics includes: body obviously sharklike, with a cylindrical trunk; snout pointed to bluntly conical and possibly depressed; head not laterally expanded; small-to-large eyes on side of head without nictitating membranes; teeth in top and bottom jaws similar or different; teeth only moderately different along a jaw; bottom teeth always with sharp cutting edge; spiracles present and sometimes large; five pairs of small gill openings just anterior to pectoral fins; pectoral fins small-to-moderate in size; two low-to-high dorsal fins with spines, as in *Squalus*, *Etmopterus*, and *Oxynotus* species or without spines as in *Isistius*, *Somniosus*, and *Eupotmicroides* species; pelvic fins small to moderate in size; anal fin absent; and caudal fin with or without dorsal notch and with ventral lobe shorter than dorsal lobe when present. At maximum size, males are generally smaller than their corresponding females. Species such as the piked dogfish (*Squalus acanthias*), which inhabit relatively shallow waters, may be counter shaded with lighter bellies, whereas those such as the pygmy shark (*Euprotomicrus bispinatus*) may be more uniform and dark. Luminous organs are possessed by a handful of species, representing genera such as *Oxynotus*, *Isistius*, *Etmopterus*, and *Centroscyllium*.

Distribution

Representatives of Squaliformes occur in all oceans. Most species are residents of temperate or tropical latitudes, where they inhabit nearshore waters associated with continental and insular shelves and slopes.

Habitat

Squaliformes are primarily found in marine environments; however, some species, such as the piked dogfish, can occasionally operate in estuarine waters. The Greenland shark has also been captured in rivers far from the sea. Such occurrences most likely represent sharks that have temporarily invaded upstream reaches by navigating the saltwater wedges associated with relatively deep tidal rivers. Squaliformes is a unique order of sharks in that at least one representative, the Greenland shark, is a common inhabitant of polar waters. Although some Squaliformes are found in the shallows, another general distinction of these sharks is their deep-water representation. In fact, most species of deep-water sharks are squaliforms, and some of them have been observed inhabiting abyssal depths. Because of this representation, it is likely that our understanding of the overall distribution of squaliforms will continue to expand as more resources are devoted to deep-sea exploration.

A newborn piked dogfish (*Squalus acanthias*) with yolk sac still attached. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

Behavior

Given their deep-water habitats, observations of many dogfish sharks in their natural surroundings only exist as valuable glimpses obtained with remote cameras and manned or unmanned deep-sea vehicles. Some species, such as many *Squalus* dogfishes, commonly roam in sizeable packs; other deep-water species, such as the lantern sharks (*Etmopterus*), probably live more solitary lives. Shark species such as the piked dogfish appear quite purposeful in their hunting activities, schooling like a marine wolf pack and devastating a wide variety of prey. Others, such as some rough sharks (*Oxynotus*) observed in deep water, seem more calculating and less voracious. A handful of these sharks, including the Greenland shark, Pacific sleeper shark, and piked dogfish, are known from both deep water and the shallows, and the cookie-cutter shark (*Isistius brasiliensis*) is thought to undertake diurnal vertical migrations in its oceanic realm. Overall, little is known about the migrations or lack thereof of most of dogfish sharks; although individuals of species such as the piked dogfish have been known to travel great distances throughout their lives.

Feeding ecology and diet

The feeding ecology of squaliforms spans that of species that feed as generalists, such as many of the dogfishes that comprise the genera *Squalus*, *Centrophorus*, and *Etmopterus*, to specialists such as the cookie-cutter sharks (*Isistius*). Because of the small size of many squaliforms, it is not surprising that small fishes and invertebrates such as various squids often make up their diet. However, their diets do include some surprises, as species such as the cookie-cutter sharks take mouthfuls from large marine animals, and huge Greenland sharks have been found with hazelnut-sized snails in their stomachs. In addition, some species, such as the Greenland shark and Pacific sleeper shark, appear to specialize somewhat by occasionally feeding on carrion, with the latter species having been filmed in deep water feeding on a decaying whale fall. The teeth of most squaliforms are not very impressive in regard to size; but they are typically well adapted for biting chunks from prey. The exceptions to this are the cookie-cutter sharks, whose teeth are proportionally some of the largest of any sharks. Little to nothing is known about the growth rate of most squaliforms, although some species grow less than 1 in (2.5 cm) per year. Similarly, the longevity of most squaliforms is unknown; however, some species are estimated to live for over 40 and possibly over 100 years. Dogfish sharks are preyed on by other sharks, teleosts, marine mammals, and humans.

Reproductive biology

The reproductive biology of these sharks is poorly known, with much knowledge stemming from several well-known species such as the piked dogfish. As in all elasmobranches, fertilization is internal, and it is suspected that all squaliforms are ovoviviparous, giving birth to live young that derive their embryonic nourishment from egg yolk, rather than from a more intimate and placenta-like maternal connection. Litters of these sharks typically yield six to 10 pups, with neonates of various species ranging from about 3–16 in (7.6–40.6 cm) long. Nursery areas are known or suspected for at least some species.

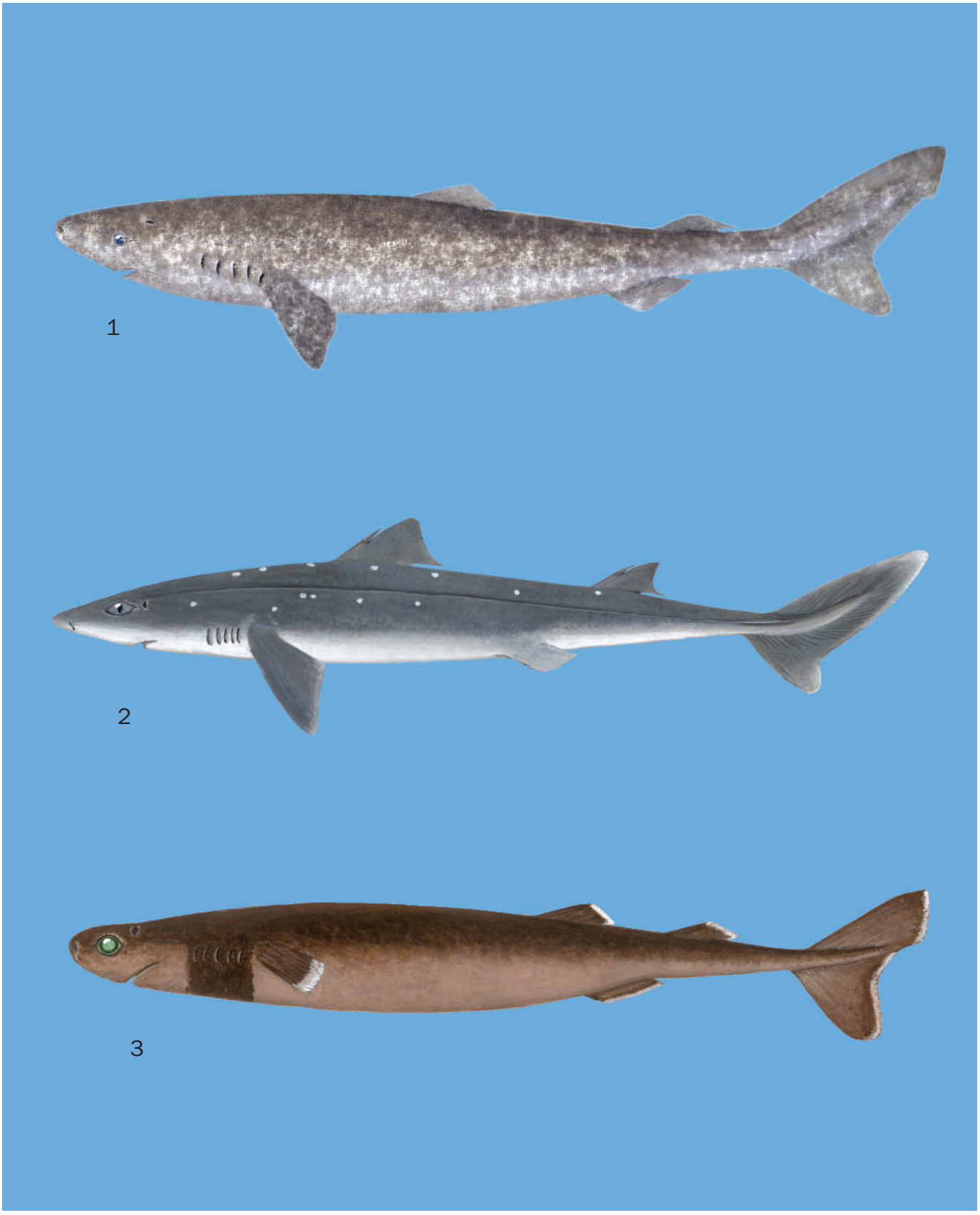
Conservation status

Three dogfish sharks are included on the IUCN Red List: the gulper shark (*Centrophorus granulosus*) is categorized as Vulnerable, the kitefin shark (*Dalatias licha*) as Data Deficient, and the piked dogfish (*Squalus acanthias*) as Lower Risk/Near Threatened. Because these sharks grow slowly and have a low reproductive output, fisheries should be able to overexploit them more easily than is possible with many other fishes. A report on the conservation status of 75 species of squaliforms published in 1999 noted 60% to be unexploited by fisheries. Of these, many are relatively small, deep-water forms such as the lantern sharks. Of the exploited species, 74% were categorized as species of unknown conservation status due to lack of information. Species in this group included many relatively deep-water forms such as gulper sharks (*Centrophorus*). The kitefin shark and the Greenland shark were considered exploited species that have limited reproductive potential and other life-history characteristics that make them especially vulnerable to overfishing. The bramble shark (*Echinorhinus brucus*) and the piked dogfish were considered the most imperiled of all squaliforms, falling into a conservation category comprised of species associated with historical declines in catches that have sometimes resulted in their being considered locally rare. Because many squaliforms live in relatively deep waters and catch statistics are lacking for many of them, the above conservation review must be deemed preliminary. But to be sure, there can be little doubt that heavily fished species such as the piked dogfish appear to be exploited to the maximum or overexploited throughout much of their range, and that fisheries management plans, some of which are being developed, will be needed to sustain fished populations. Little is known regarding the effects of pollution and habitat destruction on these sharks; however, several studies have in-

dicated some squaliforms to be heavily polluted by such chemicals as PCBs and the pesticide DDT.

Significance to humans

In summing up the significance of squaliforms to humans, it is not an exaggeration to say that these sharks have probably been more fully utilized than any other group of sharks, and possibly more so than any other group of fishes. Historically squaliforms have played a role in myth, art, cultural rituals, and medicine. They have been utilized to feed people and domestic animals throughout the world. Oil extracted from their livers has served as lantern fuel, as a cosmetic additive, and as a machine-gun lubricant. The skin of squaliforms has been used as a natural type of sandpaper, and the hides of these fishes have been tanned into durable leather. Shark teeth have been used in various ceremonial art objects, as well as functioning as cutting tools. Studies of one species in particular, the piked dogfish, have facilitated the education of countless millions of biology students and have also been responsible for a great wealth of biological understanding regarding vertebrate physiology. And surprising to many, some of these species have and are being used as bait to catch lobsters and other more desirable species of sharks. There is no authenticated record of an attack on a human by any dogfish shark, although their vicious dorsal spines have certainly painfully lanced many fishermen. Furthermore, at some times and in some areas various squaliforms have posed a great nuisance to fishing operations and have destroyed valuable fishing gear.



1. Greenland shark (*Somniosus microcephalus*); 2. Piked dogfish (*Squalus acanthias*); 3. Cookie-cutter shark (*Isistius brasiliensis*). (Illustration by Dan Erickson)

Species accounts

Cookie-cutter shark
Isistius brasiliensis

FAMILY
Dalatiidae

TAXONOMY
Scymnus brasiliensis Quoy and Gaimard, 1824, Brazil.

OTHER COMMON NAMES
English: Luminous shark; French: Squalelet féroce; Spanish: Tollo cigarro.

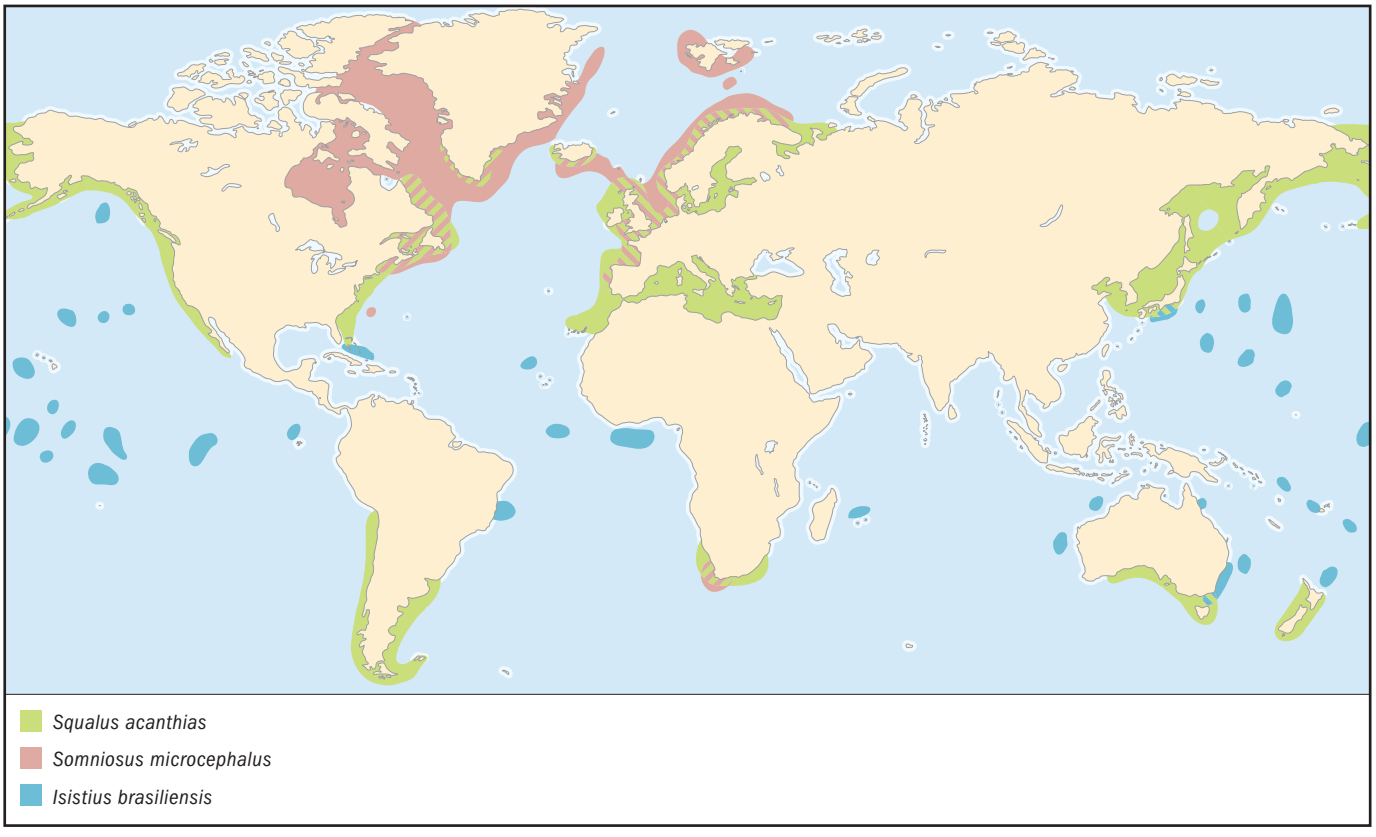
PHYSICAL CHARACTERISTICS
A small shark; females about 22 in (56 cm), males seldom longer than 16.5 in (42 cm). Body shaped like torpedo cigar, widest at about midpoint and tapered most along posterior length, dorsal surface of head slightly depressed. Snout short, eyes large, mouth with fleshy lips, massive lower jaw bearing functional edge of 25–31 large triangular teeth in a row, large spiracles located atop head behind eyes, gill slits small, pectoral fins small, two small spineless dorsal fins of approximately same size set far back on body, anal fin lacking, caudal fin prominent with nearly symmetrical lobes. Body brownish, darker dorsally than ventrally, distinctive dark collar band encircling body at level of gills, trailing margins of fins translucent. Luminescent organs casting a bright greenish glow cover ventral surface of trunk with exception of fins and dark collar band.

DISTRIBUTION
Oceanic, reported from the Indian, Pacific, and Atlantic Oceans, scattered widely throughout tropical latitudes. Less frequently reported from warm temperate regions, sometimes in association with oceanic islands.

HABITAT
Based on fishing data, utilizes a fair vertical swatch of its potential environment. Has been captured at the surface, often at night, but also seems well represented at depths between 279–11,482 ft (85–3,500 m). Based on this information and a limited knowledge of its behavior, this species may undergo diurnal bathypelagic to epipelagic migrations associated with feeding.

BEHAVIOR
Few behavioral observations exist in nature. Thought to occasionally form loose aggregations of individuals and to be a slow swimmer. Based on characteristic craterlike wounds on organisms such as marine mammals and large fishes, as well as matching plugs of tissue from stomachs of captured cookie-cutter sharks, the species is thought to feed on large prey organisms by cleanly biting a mouthful of tissue from its victims before they swim off otherwise unharmed. Because of this, the species has been considered both micropredator and parasite; technically it should be labeled a facultative parasite because it also consumes smaller prey items in their entirety.

Explanations as to how these sharks attack large organisms have been advanced since at least the mid-1800s. As of 2002, a



popular explanation points to a hunting method that employs deceit: the sharks use their luminescent abilities to counterilluminate and camouflage their ventral surface so that the striking dark collar band near the head assumes the appearance of a small prey item. Large predators drawing near to investigate this potential meal are eventually met with a quick bite before they can speed off. As convincing as this explanation may seem, it must be considered speculation until supported by observation.

FEEDING ECOLOGY AND DIET
Feeds on a variety of invertebrates and vertebrates, presumably using two behaviors: eats relatively small prey items, such as squids, crustaceans, and bristlemouths, whole or entirely in pieces; eats large prey, such as megamouth sharks, marlins, tunas, wahoos, dolphins, and other cetaceans, dugongs, and pinnipeds, by removing a single mouthful. This flexibility works well, especially in light of its oceanic distribution, where similar predators profit from the vertical and horizontal movements of prey organisms of varying sizes. It is not known if this species is routinely preyed upon by others.

REPRODUCTIVE BIOLOGY
Males mature at 15 in (38 cm); females at 15.7–18.9 in (40–48 cm). Little first-hand information is known regarding the reproductive biology; but fertilization is presumably internal and development ovoviviparous. Although gestation period, number of embryos per litter, and size at birth are unknown, 6–12 eggs have been observed in the uteri of some specimens. Distributions of smaller sharks near oceanic islands have prompted some biologists to propose that young are born in coastal areas.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Because of its small size and scattered distribution, this shark has had little fishery value. It has been reported that this vicious shark has attacked castaways and even a scuba diver; but there is little hard evidence for this. Nonetheless, given its habit of attacking prey much larger than itself, it is likely that some adventurous diver operating offshore at night will eventually be bitten. In addition, based upon characteristic bitelike holes in the neoprene boot of a hydrophone mast, this species has been implicated in otherwise uneventful attacks on a U.S. nuclear submarine. Such attacks aside, the primary significance of this species to humans lies in its ability to astound with its ferocious design and devious behavior. ◆

Greenland shark
Somniosus microcephalus

FAMILY
Somniosidae

TAXONOMY
Squalus microcephalus Bloch and Schneider, 1801, glacial seas ("Habitat in mari glaciali").

OTHER COMMON NAMES
English: Ground shark, gray shark, gurry shark, sleeper shark; French: Laimargue du Groenland, leiche; German: Eishai; Spanish: Tollo de Groenlandia; Dutch: Apekalle, havkel; Inuktitut: Ekalugssuak, eqaludjuaq, iqalugjuaq; Norwegian: Haakjaerring.

PHYSICAL CHARACTERISTICS
Large, stocky species; females at least 21 ft (6.4 m) and weighing 2,250 lb (1,020 kg), males typically smaller but at least 11 ft (3.3 m). Body "torpedo" shaped, head conical with blunt snout bearing large olfactory openings, body widest at about level of pectoral fins, eyes often infected by conspicuous parasitic copepods, spiracles obvious, mouth suctoral, lower jaw bearing a functional edge consisting of 48–53 teeth whose oblique cusps virtually overlap to form a continuous cutting edge, gill slits small, pectoral fins paddlelike, two spineless dorsal fins about equal size, anal fin lacking, caudal keels present, caudal fin semilunate and appearing powerful. Body brownish, purplish, or bluish gray, sometimes mottled by irregular spots, ventral surface minimally lighter than dorsum.

DISTRIBUTION
Polar and temperate seas, from high latitudes well above the Arctic Circle in waters adjoining the Atlantic Ocean to at least as far south in the Atlantic Ocean as 32°N on the Blake Ridge, approximately 230 mi (370 km) off the coast of Savannah, Georgia, United States. Most common north of Cape Cod, United States, in the western Atlantic and north of Great Britain in the eastern Atlantic. There are no incontrovertible records of Greenland sharks from the Southern Hemisphere or from the Pacific or Indian Oceans, although other sleeper sharks of the genus do inhabit those waters.

HABITAT
The only well-documented sharks to inhabit the Arctic, common in waters below 32°F (0°C) that are seasonally covered by sea ice. In northern portions of the range these sharks can be found lurking below landfast ice, or in open water at depths exceeding 500 ft (152 m), or in knee-deep shallows. At more southerly latitudes, they are usually only seen during the winter. However, this species probably goes unnoticed, residing year-round in cold, deep waters, where it has been seen at depths as great as 7,218 ft (2,200 m). These sharks may occasionally inhabit brackish waters, as indicated by reliable reports of individuals captured over 50 mi (80 km) upstream in the Saguenay River in Quebec, Canada.

BEHAVIOR
Somniosus means "sleeper" in Latin, and certainly this shark lives up to its name. Accounts of the lethargic nature of this fish are widespread, including accounts of them being hauled up on hooks with hardly a fight. In describing fresh-caught specimens, Hansen (1963) wrote, "owing to the sluggishness of this fish, it could sometimes be a little difficult to judge if it was dead or alive." How this most sluggish species is capable of catching swift prey such as chars and seals remains a mystery. Although it has never been observed, some Norwegian fisherman believed that a brightly colored parasitic copepod that infects the eyes of many of these sharks might serve as a lure to attract curious prey within striking distance. Nonetheless, those copepods do appear to cause enough damage to the eyes such that one might surmise that this shark does not rely on keen vision to capture its dinner. In some instances sound or olfaction may be the key, and fishing, sealing, and whaling operations have been noted to attract them.

FEEDING ECOLOGY AND DIET
The examination of stomach contents and studies of stable isotopes indicate that these sharks feed at a number of trophic levels, and while they can swallow smaller prey whole, they also feed in a piecemeal fashion by scooping large, melon ball–like chunks from larger items. Their diet has included jellyfishes, brittle stars, sea urchins, amphipods, crabs, snails,

squids, and seabirds; a variety of fishes such as small sharks, skates, herrings, chars, salmons, eels, capelins, redfishes, sculpins, lumpfishes, cods, haddock, wolfishes, and halibuts; as well as marine mammals such as seals and narwhals. As well as preying on live organisms, these sharks are well known to gluttonously consume animals compromised by fishing gear, along with almost any carrion. The latter habit prompted whalers to give them the unflattering name of gurry or "garbage" sharks. In some areas the flesh is toxic to both humans and dogs, and must be properly prepared before consumption. In addition, the flesh of some sharks is heavily contaminated with persistent organic pollutants that probably enter the sharks via their diet. Although this species will eat others of its kind that are compromised by fishing gear, it is not known whether it is normally preyed upon by species other than humans. Limited growth data on these sharks suggests they grow slowly and that some individuals may live for over 100 years.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of this species; but presumably fertilization is internal and development is ovoviviparous. Information regarding age at first maturity, gestation period, numbers of embryos per litter, and size at birth are nonexistent, except for some information from a single report of a 16 ft (5 m) long female that contained 10 embryos. The pups appeared full term and the single embryo measured was about 14 in (36.7 cm) long. Based on maximum size, males probably mature at a smaller size than females. Given the great size of this species and the tendency for it to eat anything in its path, it is possible that shallow nursery areas segregate neonates and juveniles from adults.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Regardless of its large size, this species is inoffensive to humans, and no authenticated attacks have been reported. This fish has been employed in various ways by Inuit communities; the flesh consumed by humans and sledge dogs, the liver providing a fine oil, the teeth and rough skin used for cutting and scraping. Europeans, Greenlanders, and Icelanders have also fished the species for similar purposes. Directed commercial fisheries existed from about the mid-1800s until about the mid-1900s. Other than relatively small numbers taken by some traditionalists, most captured today are probably taken as bycatch in fisheries directed at other fishes such as turbots. In some areas these sharks have been so numerous and destructive to fishery equipment and operations that they have been looked upon as a nuisance and were sometimes targeted by operations aimed at reducing their abundance. ◆

Piked dogfish
Squalus acanthias

FAMILY
Squalidae

TAXONOMY
Squalus acanthias Linnaeus, 1758, European sea ("Oceano europaeo").

OTHER COMMON NAMES
English: Grayfish, spiny dogfish, spurdog; white-spotted spurdog; French: Aiguillat commun; German: Gemeiner dornhai; Spanish: Mielga; Danish: Pighai; Dutch: Dornhaai; Norwegian: Pighaa.

PHYSICAL CHARACTERISTICS
A small shark; total length of females 4 ft (120 cm), weight up to 21.6 lb (9.8 kg); total length of males 3 ft (160 cm). Body quintessentially sharklike, snout narrow, eyes large, spiracles present, mouth with similarly shaped teeth in top and bottom jaws, 28 teeth in top jaw and 22–24 teeth in bottom jaw, first and second dorsal fins each bearing a dorsal spine, second dorsal spine more pronounced than first, anal fin lacking, caudal keels present, caudal fin without subterminal notch on upper lobe. Dorsal surface of body usually slate-colored, flanks each with a row of small white spots that are most conspicuous on younger fish, ventral surface light gray to white.

DISTRIBUTION
Antitropical marine and estuarine waters throughout the Atlantic and Pacific Oceans and adjoining seas, encompassing boreal to warm-temperate waters in the Northern Hemisphere and antiboreal to warm-temperate regions in the Southern Hemisphere.

HABITAT
Inhabits inshore and offshore waters associated with continental and insular shelves. Given its migratory nature and widespread abundance, this small dogfish utilizes a broad scope of habitats. Can be found as in waters as shallow as the intertidal zone, although may venture as deep and probably deeper than 2,952 ft (900 m). Seem to prefer waters about 42–46°F (6–8°C); however, tolerates up to 59°F (15°C). May make short upstream incursions utilizing the saltwater wedges of tidal rivers.

BEHAVIOR
Although they cannot be characterized as being swift, these sharks are strong swimmers and can maintain a steady cruising pace. Gregarious fishes, they typically gather and migrate in large schools consisting of equally sized individuals. Schools of large adult females tend to be more common inshore; schools of juveniles are more common offshore. In the northwestern Atlantic Ocean, their north-south seasonal migration usually places them in the northernmost part of their range near Labrador by early fall, and in the southernmost part of their range off the Carolinas to northeastern Florida by midwinter. In addition to these seasonal movements, they also exhibit general movements inshore during warmer months and movements offshore as it gets colder. Tagging studies have shown that some journey over long distances, with certain transoceanic wanderings in the North Atlantic and North Pacific Oceans totaling 994–4,039 mi (1,600–6,500 km).

FEEDING ECOLOGY AND DIET
Typically feeds in packs, often moves into an area and lays waste to or drives off most fishes. In any wide portion of their range, fishes usually constitute the largest percentage of the diet, followed by squids and other invertebrates. A list of stomach contents would mimic a relatively thorough inhabitant list for many waters. In the northwestern Atlantic Ocean, small schooling fishes such as herrings, menhadens, capelins, sand lances, and mackerels offer them ample opportunity to gorge. Although their relatively small size limits their lethal abilities, fishes as large as cods and haddocks can fall prey to these ravenous squaliforms. Because of their vast appetites, these fishes can grow about 0.6–1.4 in per year (1.5–3.5 cm), and estimates of their longevity based on the interpretation of growth rings on their spines are commonly about 40 years, but may be as long as 100 years. Because of their relatively small size, they

are preyed upon by large sharks and teleosts, seals, killer whales, and of course, humans.

REPRODUCTIVE BIOLOGY

More is known about the reproductive biology of this fish than about that of any other shark, skate, or ray. Males reach maturity at about 11 years old, females at 18–21 years. Fertilization is internal, development is ovoviviparous, and gestation may last from 18–24 months. Litter size ranges from 1–15 pups; however, six or seven is typical. At birth the neonates are usually about 10 in (26 cm) long.

CONSERVATION STATUS

Considered to be overexploited in many regions and listed by the IUCN as Lower Risk/Near Threatened. However, in many parts of its range, this is probably the most abundant shark, and can be so common that within the Gulf of Maine, to "mention all the localities from which they have been reported would be simply to list every seaside village and fishing ground from Cape Cod to Cape Sable" (Bigelow and Schroeder, 1953).

SIGNIFICANCE TO HUMANS

Almost anyone who has taken an advanced course in biology has toiled to locate the cranial nerves of these fishes. Their flesh has been eaten fried (as in "fish and chips"), broiled, and baked by humans, and ground into meal for pet food. They have also been the bane of many commercial fisheries for driving valuable catches away, beating other fishes to the bait, and ruining nets full of keepers. Furthermore, they can administer a merciless sting with their sharp spines. ◆

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George W. Benz, PhD

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Squatiniformes
(*Angelsharks*)

Class Chondrichthyes
Order Squatiniformes
Number of families 1

Photo: The Pacific angelshark (*Squatina californica*) is well camouflaged when lying on the sandy ocean bottom. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Angelsharks are an ancient lineage, first appearing in the fossil record about 150 million years ago during the late Jurassic period. The remains of articulated angelsharks are known from the marine deposits of Solnhofen, southern Germany (genus *Pseudorhina*); these are well-preserved specimens that resemble modern angelsharks in most morphological details. Most fossil angelshark species, however, are known from isolated teeth reported from the late Jurassic to the Pliocene epoch (some 5 million years ago) of many localities, including Europe, North America, Greenland, Japan, and Africa.

The evolutionary relationships of angelsharks have been intensely debated since their discovery. They are presently classified in a large group with the cow and frilled sharks (Hexanchiformes), the dogfishes and allies (Squaliformes), the sawsharks (Pristiophoriformes), and the rays (also known as batoids). Together, these groups comprise the Squalea, as all members have complete hemal arches (ventral projections arising from the vertebral column) in the trunk region anterior to the tail, among other anatomical innovations. Within the Squalea, the angelsharks are most closely related to a group that includes the sawsharks and the rays. Angelsharks have traditionally been thought to be closely related to rays, but rays are actually more closely related to sawsharks. Almost nothing is known about the phylogenetic relationships among angelshark species. All living angelsharks are classified together in one family, the Squatinidae.

Fifteen living species of angelsharks are currently recognized, all placed in the single genus *Squatina*. There may also be two undescribed species living off southern Australia. Most living species of angelsharks have not been very well characterized, and critical taxonomic studies are still needed. Much is yet to be learned about their population dynamics and reproductive patterns, which are essential because some species are of commercial importance locally (for example, in Australia).

Physical characteristics

Angelsharks are among the most distinctive living sharks, strongly resembling rays in being dorsoventrally flattened, with enlarged pectoral fins reminiscent of the batoid disc. The head of angelsharks, however, is not fused to the pectoral fins as it is in rays (where it forms the disc). Their pectoral fins have a unique anterior lobe that mostly conceals the five gill slits. The gill slits are laterally situated, but extend ventrally as well (contrasting to the exclusively ventral gill slits of rays). The head is exceptionally wide and depressed, entirely anterior to the pectoral fins, and with a very wide, terminal mouth. The eyes and spiracles are dorsally situated, close to the front margin of the head, and the spiracles are somewhat transverse. The anterior nasal flaps are wide and fringed, and the pattern of fringes is sometimes useful in identification. Angelsharks have two spineless dorsal fins posterior to the pectoral and pelvic fins, a rather slender, short tail that is abruptly demarcated from the trunk, a caudal fin that is unique in having a greatly elongated lower lobe (longer than upper lobe), and no anal fin.

Coloration is diagnostic for many angelshark species. Some have a relatively light background color, but others are darker, and most are marked with various spots, ocelli (eyelike spots), and blotches, sometimes of varying color and size. *Squatina tergocellata* from Australia has three pairs of characteristic dark ocelli on its back and pectoral fins, and *S. tergocellatoides* from Taiwan has similar spots dorsally, but not quite forming ocelli. *Squatina australis* is unique in presenting dark spots on the lower lobe of its caudal fin, with creamy white and darker

spots dorsally. *Squatina japonica* is reddish dorsally (as is *S. squatina*) with darker red blotches over the trunk. The southwestern Atlantic species are similar to each other in coloration, composed of a dark or light tan background with yellowish and brownish spots and diffused blotches.

Angelsharks are mostly of medium size, reaching about 5 ft (1.5 m) long, but occasionally larger individuals, up to 6.6 ft (2 m), may occur. For most species, males mature when between 29.5–43.3 in (75–110 cm), and females at slightly larger sizes. Size at birth varies from 9.8–13.8 in (25–35 cm).

Distribution

Angelsharks occur almost worldwide, but most species are geographically restricted. *Squatina californica* occurs in the eastern Pacific; three species are Mediterranean (*S. squatina*, *S. oculata*, and *S. aculeata*), also occurring along the western African coast (the latter two down to Namibia); four species are found in the western Atlantic (*S. dumeril*, *S. argentina*, *S. guggenheim*, and *S. occulta*); *S. africana* occurs in the Indian Ocean; *S. tergocellata* and *S. australis* occur off southern Australia; and four species are western Pacific (*S. tergocellatoides*, *S. nebulosa*, *S. japonica*, and *S. formosa*).

Habitat

Angelsharks occupy the continental shelf and upper slope regions, in depths ranging from just several feet (1.5 m to 150 m) down to about 4,265 ft (1,300 m), but most species are found inshore. They usually occur on sand, mud, and gravel substrates.

Behavior

Angelsharks frequently bury themselves in sandy or muddy bottoms, as do many rays, in order to ambush their prey or to rest during the day (they are primarily nocturnal). Burial is accomplished by a vigorous "flapping" of the pectoral fins, which raises the sediment. Dorsal eyes and spiracles allow angelsharks to breathe regularly while waiting for their prey to pass by, as water may reach the gills through the enlarged spiracles. The top of the head and trunk are frequently left exposed. Angelsharks are ambush predators. As prey items have to be of the right size, angelsharks may remain concealed in an immobile state for long periods, waiting for the proper prey to pass close to their mouths. Capture of prey is done in a very swift, high-speed maneuver, in which the anterior part of the body is abruptly uplifted; the prey is ingested whole after being properly adjusted in the mouth.

Feeding ecology and diet

Angelsharks eat a wide variety of invertebrates and fishes. Their capacious mouths allow them to ingest prey items of substantial size. Crustaceans, cephalopods, bivalves, and bony fishes are commonly consumed, as well as other sharks and rays; one specimen was observed to spit out a newly born bullhead shark immediately after ingesting it, probably because of its finspines.

Reproductive biology

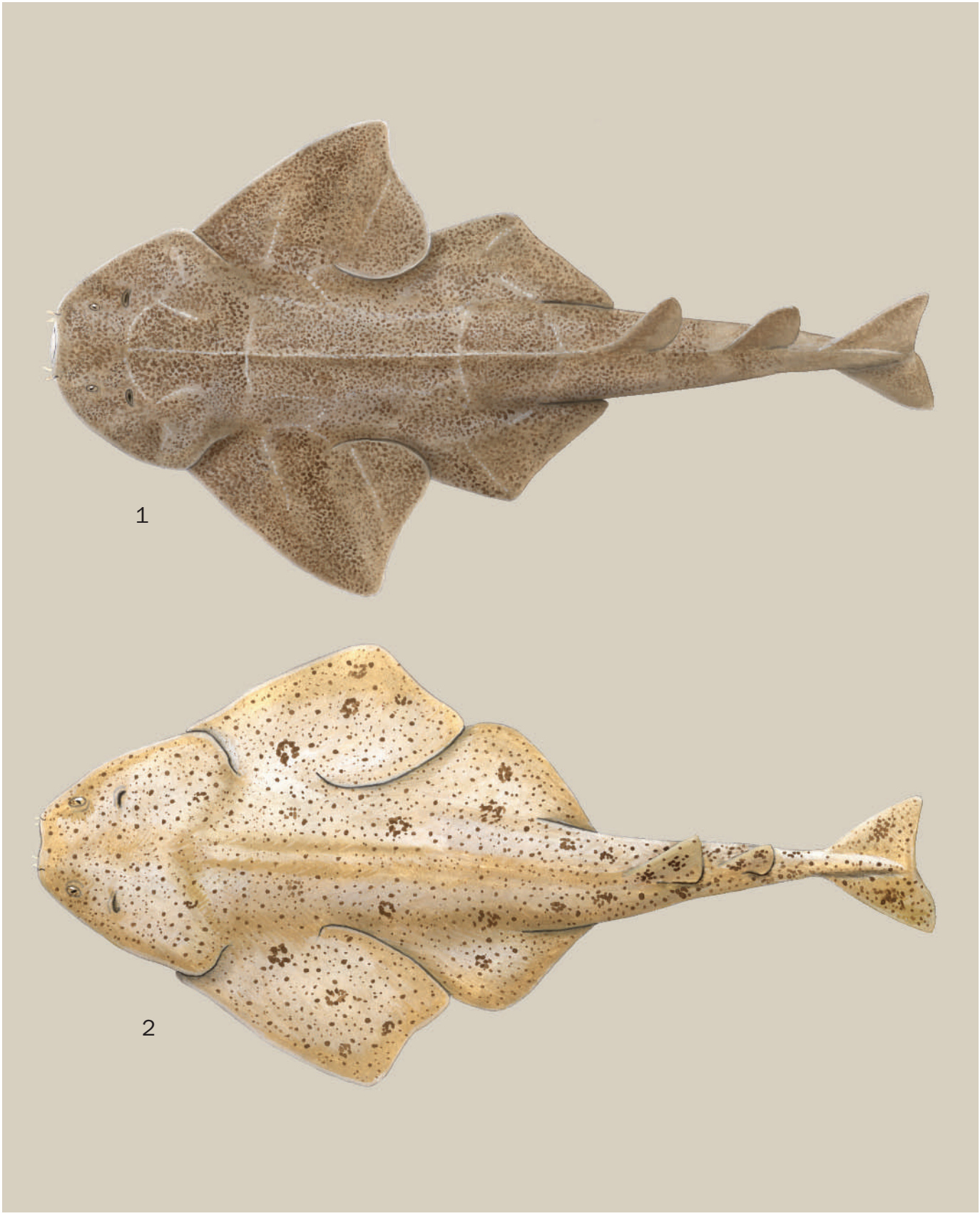
All angelsharks are ovoviviparous (aplacentally viviparous; giving birth to live young), and have internal fertilization, as do all sharks, rays, and chimaeroids (Chondrichthyes). Gestation periods are mostly unknown, but appear to be about 10 months for one species, *S. californica*. Litter sizes vary between one and 20 pups per gestation, and the young measure around 9.8 in (25 cm) when born. Southwestern Atlantic angelsharks employ cloacal gestation, in which the fully developed fetus remains, prior to birth, in a small chamber (posterior to the uterus) that opens into the cloaca; this occurs during the second half of the gestation period and lasts for several months.

Conservation status

Five species of angelsharks are listed by the IUCN. *S. occulta* is Endangered; the Brazilian subpopulation of *S. guggenheim* is listed as Endangered, while the rest of the species is Vulnerable; *S. squatina* is Vulnerable; *S. californica* is Lower Risk/Near Threatened; and *S. argentina* is Data Deficient.

Significance to humans

Angelsharks pose little direct threat, because of their size, habits, and vertical distribution. However, caution is necessary, as angelsharks have sharp teeth and strong jaws and have been known to defend themselves if provoked. They are consumed on a regular basis as food (fresh, frozen, or salt-dried), especially in the western Pacific (*S. japonica*), Australia (mainly *S. australis*), and in the eastern Pacific (*S. californica*). Their skin is also used for polishing wood surfaces and as sharkskin leather (consisting of the dried skin with denticles). They are caught as bycatch in bottom trawls.



1. Angelshark (*Squatina squatina*); 2. Pacific angelshark (*Squatina californica*). (Illustration by Dan Erickson)

Species accounts

Pacific angelshark
Squatina californica

FAMILY
Squatinidae

TAXONOMY
Squatina californica Ayres, 1859, California.

OTHER COMMON NAMES
English: California angelshark; Spanish: Pez ángel del Pacífico.

PHYSICAL CHARACTERISTICS
Pacific angelsharks present rather simple, spatulate, nasal flaps (not intensely fringed), and a light-brown background with small dark brown spots and blotches, mostly smaller than spiracle-diameter, scattered over the trunk and tail. There is a row of small denticles along the back and tail, and also in between the dorsal and caudal fins, and small spines are also present on the snout and around eyes.

DISTRIBUTION
These sharks occur from Alaska to the Gulf of California, and from Ecuador to Chile. South American occurrences may refer to a distinct species, presently not recognized. They are abundant close to the Channel Islands (California).

HABITAT
Pacific angelsharks inhabit shallow, nearshore waters, down to 164 ft (50 m) off the California coast, but to about 590.5 ft (180 m) in the Gulf of California, over rocky, muddy, and sandy bottoms, and near kelp forests.

BEHAVIOR
Pacific angelsharks are sluggish and mostly nocturnal. Adults are somewhat nomadic, spending brief periods in restricted areas of about 1 sq mi (2.6 sq km) before moving to a new region several miles distant. Although these sharks are mostly solitary, small aggregations have been observed.

FEEDING ECOLOGY AND DIET
These sharks eat fishes (croakers, blacksmith, and halibut), shrimp, squid, and squid egg cases. They also feed on the peppered catshark (*Galeus piperatus*) in the Gulf of California.

REPRODUCTIVE BIOLOGY
Male Pacific angelsharks mature at about 29.5–31.5 in (75–80 cm), females at slightly greater sizes. Pups are born at about 7.9–13.8 in (20–25 cm). Litter size ranges from a single offspring to 13, and the gestation period is reported to last 10 months. Birth occurs in March and June.

CONSERVATION STATUS
California angelsharks are listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
These sharks are consumed fresh or frozen in California, and especially in areas near the Gulf of California. They are also consumed off western South America. Not usually kept in aquaria, Pacific angelsharks are one of the most commonly observed angelsharks in the wild. ◆

Angelshark
Squatina squatina

FAMILY
Squatinidae

TAXONOMY
Squalus squatina Linnaeus, 1758, Mediterranean Sea ("Oceano Europaeo").

OTHER COMMON NAMES
English: Common angelshark; French: Ange de mer commun, Spanish: Angelote.

PHYSICAL CHARACTERISTICS
Squatina squatina is distinguished by having a long tentacle on its spatulate, unfringed nasal flap, and a dorsal coloration composed of a gray, yellow, or light-brown background, mottled in dark, minute spots. There are few denticles scattered along the midline, as well as on the snout and around the eyes.

DISTRIBUTION
Mediterranean, eastern Atlantic, bordering the United Kingdom to Scandinavia, also in the Shetland Islands, and south to Morocco and the Canary Islands.

HABITAT
These sharks inhabit shallow inshore waters, from 5 ft (1.5 m) down to 492 ft (150 m). Found on rocky, gravely, muddy, and sandy bottoms.

BEHAVIOR
Squatina squatina is mostly nocturnal. Adults are known to migrate northward in the summer in northern parts of the distribution.

FEEDING ECOLOGY AND DIET
Eats fishes (hake, argentines, flatfishes, and skates), crabs, shrimp, and mollusks.

REPRODUCTIVE BIOLOGY
Female angelsharks mature at about 49.2 in (125 cm), males at slightly smaller sizes. Pups are born at about 9.4–11.8 in (24–30 cm). Litter size ranges from seven to 25, depending on the size of the mother. Females give birth in the summer months in the colder part of the range, but during the winter in the Mediterranean.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Angelsharks are consumed fresh, frozen, or salt-dried; and are possibly utilized for fish oil and fishmeal. ◆

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Marcelo Carvalho, PhD

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Pristiophoriformes
(Sawsharks)

Class Chondrichthyes
Order Pristiophoriformes
Number of families 1

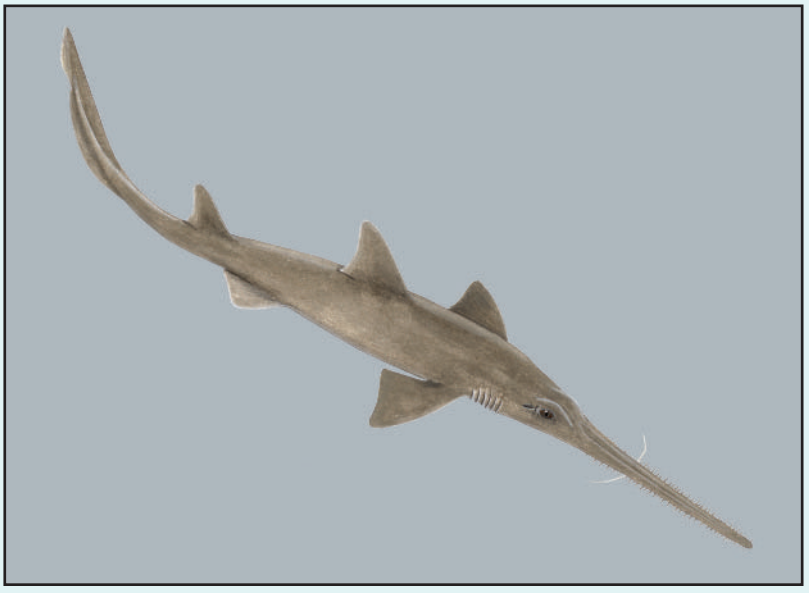


Illustration: Common sawshark (*Pristiophorus cirratus*). (Illustration by Dan Erickson)

Evolution and systematics

Sawsharks first appear in the fossil record during the late Cretaceous period (some 85 million years ago [mya]) in Lebanon in the form of more or less complete fossils, but almost all sawshark fossils consist of isolated remains of rostral spines from the Tertiary period (from between 65 and 5 mya). Sawshark fossils are not very common, but indicate that they were once more widespread, at least in the Pacific, southern and northeastern Atlantic, as remains have been found in Japan, Africa, Europe, New Zealand, and North and South America.

Sawsharks are closely related to the cow and frilled sharks (Hexanchiformes), the dogfishes and allies (Squaliformes), the angelsharks (Squatiniformes), and the rays (or batoids). Together these groups comprise the Squalea, as all members have complete hemal arches (ventral projections arising from the vertebral column) in the trunk region anterior to the tail, among other unique anatomical features. Within the Squalea, the sawsharks are most closely related to the rays. All sawsharks are classified in the family Pristiophoridae.

There are two genera of living sawsharks, *Pliotrema* and *Pristiophorus*. *Pristiophorus* has four included species, but *Pliotrema* is monotypic (that is, only a single species, *P. warreni*, is recognized). The phylogenic relationships among sawshark species have not been investigated. Their taxonomy is still poorly known, mainly as a result of the paucity of specimens available for study from many regions. Two putatively new species of sawsharks have been reported from Australia. Their general biology is also inadequately known.

Physical characteristics

Sawsharks are readily identified by their slender, slightly depressed body, which is preceded by a very elongated toothed "saw." The saw (or "rostral saw") is an anterior, hypertrophied extension of the snout region (rostrum). The saw has large, sharp, lateral rostral spines, which are replaced continuously through life, as well as a pair of long, ventrally extending barbels that are well anterior to the nostrils. The mouth and nostrils are entirely on the ventral surface. Sawsharks lack an anal fin, have relatively large pectoral and spineless dorsal fins, and a low, long caudal fin. The eyes and spiracles are large.

Sawsharks are sometimes confused with the sawfishes (Pristidae), a group of rays that also have elongated rostral saws. However, both groups are easily distinguished, as sawfishes (rays) do not present rostral barbels, have rostral teeth of equal size that grow continuously (as opposed to sawshark rostral spines which are replaced when broken off, and vary in size), and have ventral gill slits. There are numerous other anatomical differences, such as the arrangement of canals for the passage of vessels and nerves within the rostral saw, and the mode of attachment of rostral spines (which are not embedded in the saw in sawsharks, as they are in sawfishes).

The genera of sawsharks (*Pliotrema* and *Pristiophorus*) are easily distinguished. *Pliotrema* has six gill slits, whereas *Pristiophorus* has five (gills slits in all sawsharks are lateral, just anterior to the pectoral fins), and the rostral spines of *Pliotrema* bear small serrations on their posterior margins. Most species of sawsharks are drab and gray colored, with the exception of the more ornately colored *P. cirratus*.

Sawsharks are small to average in size, reaching about 55 in (140 cm) in length. Most species are born at about 9.8–13.8 in (25–35 cm). The size at sexual maturity is poorly known, but has been established to be around 32.7 in (83 cm) for males for at least one species, *P. warreni*, and slightly larger for females.

Distribution

As far as is known, sawsharks have a restricted distribution in tropical and warm-temperate waters, occurring in the western Pacific Ocean (Philippines, Japan, and China; *P. japonicus*), western Indian Ocean (southeastern Africa; *P. warreni*), southern, western, and eastern Australia (*P. nudipinnis* and *P. cirratus*), and also in the western North Atlantic, around the Bahamas, and between Cuba and Florida (*P. schroederi*).

Habitat

Most sawshark species inhabit the continental shelf region, but some species are also present along the continental slope in waters as deep as 3,002 ft (915 m), and one species, *P. schroederi*, is known only from deep waters. Some species present great depth variation, occurring in shallow bays but also along the upper slope. Sawsharks are generally found on soft gravely or sandy bottoms.

Behavior

Sawsharks, similar to the sawfishes (rays), utilize their saw to stun and kill fish by swinging it from side to side, and also to stir up bottom sediments when hunting. The rostral barbels may contain taste buds, and the saw is heavily endowed with sensory receptors (ampullary pores, which detect electrical fields, and lateral-line pores, which detect physical perturbations in the water). Some species are rather abundant, occurring in large groups, perhaps for feeding purposes, and may also present segregation of individuals according to age.

Feeding ecology and diet

Sawsharks feed mostly on fishes, but also on invertebrates such as squid and crustaceans.

Reproductive biology

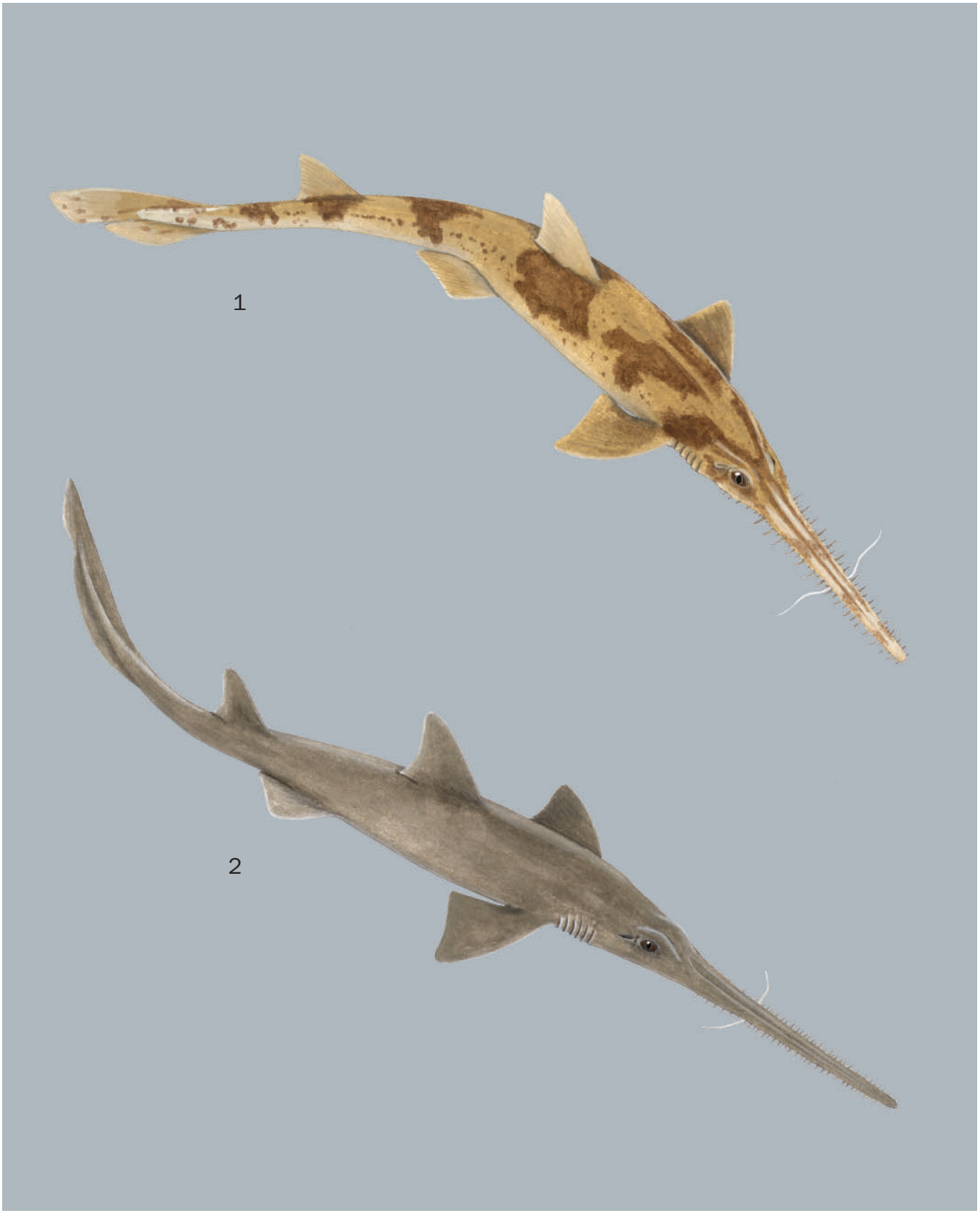
All sawsharks have internal fertilization (as do all chondrichthyans), are ovoviviparous (or aplacentally viviparous), giving birth to from seven to 17 young, but little is known about the length of their gestation periods. Young feed on yolk from the yolk sac until birth. The rostral spines are concealed in embryonic sawsharks, oriented backward so as to not harm the mother (but still very sharp), and become perpendicularly oriented only after birth. Fetal individuals present elongated rostral barbels, proportionally much longer than adults.

Conservation status

The common sawshark (*P. cirratus*) is listed as Lower Risk/Near Threatened by the IUCN.

Significance to humans

Sawsharks are consumed locally as food at least in the western Pacific (*P. japonicus*), and in Australia (*P. cirratus*), being caught as bycatch during bottom trawls. They are not usually kept in aquaria. Sawsharks pose little threat to humans, due primarily to their more obscure habits and depth distribution, but the rostral spines are quite sharp even in late-term embryos or juveniles, and may easily cause injury if handled.



1. Common sawshark (*Pristiophorus cirratus*); 2. Sixgill sawshark (*Pliotrema warreni*). (Illustration by Dan Erickson)

Species accounts

Common sawshark
Pristiophorus cirratus

FAMILY
Pristiophoridae

TAXONOMY
Pristis cirratus Latham, 1794, Australia (Port Jackson, New South Wales).

OTHER COMMON NAMES
English: Longnose sawshark; French: Requin scie à long nez; Spanish: Tiburòn sierra trompudo.

PHYSICAL CHARACTERISTICS
Common sawsharks are uniquely pigmented, with a reddish brown background pattern; numerous irregular darker brown saddles along the trunk, fins, and head; dark brown stripes across rostral saw; as well as numerous small spots (smaller than the eye) scattered on body; the rostral spines have dark margins. Ventrally uniform creamy white. Rostral saw is relatively long and slender when compared to the other Australian species, *P. nudipinnis*, and the rostral barbels are located at about the center of the rostral saw, as opposed to slightly closer to the eyes as in the latter species.

DISTRIBUTION
Common sawsharks occur off southern and western Australia (reaching to about 30°S), including around Tasmania.

HABITAT
These sharks are found on the continental shelf and upper slope, from 131–1,017 ft (40–310 m), usually on sandy bottoms. They are also reported to occur in bays and estuaries, but are believed to be more abundant from 121–479 ft (37–146 m). Although present in the same general area as *P. nudipinnis*, *P. cirratus* apparently occupies deeper waters.

BEHAVIOR
Common sawsharks are believed to form schools (perhaps for feeding) and are abundant in trawls for benthic fishes. This species has been filmed swinging its saw from side to side in an attempt to injure small fishes. They commonly rest on the bottom, with the rostral saw slightly elevated and supported in a tripodlike stance by the rostral barbels. Common sawsharks are not frequently observed in the wild.

FEEDING ECOLOGY AND DIET
These sharks feed on fishes, including cornetfishes (Fistulariidae), and on invertebrates, particularly crustaceans.

REPRODUCTIVE BIOLOGY
Mostly unknown, but they are reported to breed during winter months. Their size at birth is about 15 in (38 cm), and males are sexually mature at about 3.3 ft (1 m) in length.

CONSERVATION STATUS
These fishes are listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Common sawsharks are captured as bycatch by trawlers and are available regularly in fish markets. The flesh is reported to be very good. The elongated rostral saw is sometimes coveted for its value as an ornament. ◆

Sixgill sawshark
Pliotrema warreni

FAMILY
Pristiophoridae

TAXONOMY
Pliotrema warreni Regan, 1906, South Africa (Natal and False Bay).

OTHER COMMON NAMES
English: Sawshark; French: Requin scie flutian; Spanish: Tiburòn sierra del cabo.

PHYSICAL CHARACTERISTICS
Sixgill sawsharks are unique in having six gill slits. The rostral saw is relatively elongated, and the rostral barbels are much closer to the mouth than to the rostral tip. The sharks are pale brown dorsally. At birth they measure 13.8 in (35 cm). They reach about 55 in (140 cm), the males maturing at about 32.7 in (83 cm), and the females at 43.3 in (110 cm).

DISTRIBUTION
Southeastern Africa, from Cape Agulhas (South Africa) to Mozambique and Madagascar. *P. warreni* is the only sawshark species in the western Indian Ocean.

HABITAT
These sharks are found on the continental shelf and upper slope, from 197–1,481 ft (60–430 m). Reported to occur in deeper depths (below 361 ft/110 m) off Natal, South Africa.

BEHAVIOR
The behavior of these sharks is not well known, but they presumably use their rostral saw like other sawsharks—to stun, dig out, and kill prey. The adults are partially segregated from the young by occupying deeper waters in at least one area (off Natal).

FEEDING ECOLOGY AND DIET
Sixgill sawsharks feed on a variety of fishes (eels, hake, and gapers) as well as shrimp and squid.

REPRODUCTIVE BIOLOGY
The litter size is five to seven per gestation, but much is yet to be learned about its reproductive biology.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sixgill sawsharks are occasionally captured as bycatch and consumed locally.

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Marcelo Carvalho, PhD

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Rajiformes
(Skates and rays)

Class Chondrichthyes
Order Rajiformes
Number of families 20

Photo: A largespot river stingray (*Potamotrygon faulkneri*) is well camouflaged on a river bottom in Brazil. (Photo by Dante Fenolio/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

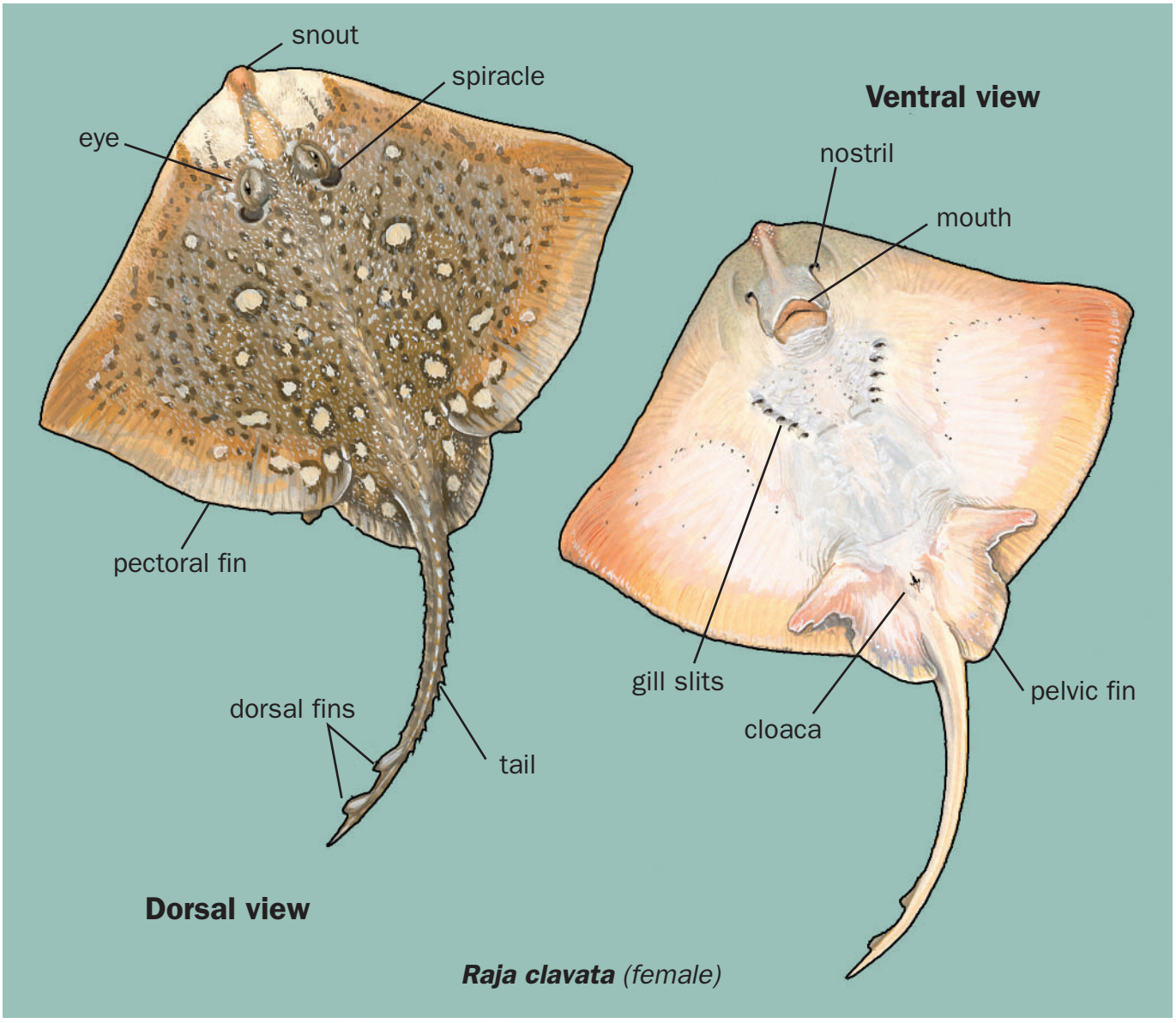
Despite the fact that skates and rays greatly outnumber their shark relatives within Chondrichthyes, they have received far less recognition. As of 2002 there were about 513 recognized species of skates and rays, compared with about 390 species of sharks. Sharks are topics of books, television documentaries, and news coverage, whereas skates and rays get little press.

Skates and rays, sharks, and chimaeroids are members of Chondrichthyes, the cartilaginous fishes. The cartilaginous fishes are distinguished from other jawed fishes (Osteichthyes, or bony fishes) by several characters. (1) The endoskeleton consists of calcified cartilage. (2) The tooth-bearing jaws are the palatoquadrate and Meckel's cartilages, rather than being comprised of dermal bones. (3) Lungs and swim bladders are absent. (4) A single boxlike skull supports the brain and sense organs. (5) Males possess copulatory organs that are extensions of the pelvic girdle and internally fertilize the females. (6) Fins are supported by elastic connective tissue rays, or ceratotrichia. (7) The body is covered with dermal denticles or placoid scales, toothlike structures with enameloid crowns and dentine bases.

Rajiformes include the electric rays, sawfishes, guitarfishes, skates, and stingrays; their fossil record dates back to the Lower Jurassic (150 million years ago [mya]) (guitarfishes). All of the major taxa are known by the Upper Cretaceous (100 mya) to the Paleocene (50 mya). A majority of the early fossils come from northern Africa and southern Europe, areas that in the late mid-Mesozoic and Lower Cenozoic were part of the Tethys Sea, a shallow tropical sea that separated the northern and southern continents over much of this period. Although the fossil record spans more than 150 million years, the record is very incomplete, owing to the paucity of hard body parts of skates and rays. Unlike the bony fishes, skates and rays (and all chondrichthyans for that matter) lack large bony external and internal structures that readily fossilize. In many cases, the fossil chondrichthyans are represented solely by teeth or enlarged scales. Teeth and scales serve to identify the fossils as skates and rays but provide little information on body structure or phylogenetic relationships.

Skates and rays have been classified variously within the cartilaginous fishes. Traditionally, they have been considered an equivalent group or sister group of the sharks. More recently, they have been grouped within a subsection of the sharks. Currently, based on morphological characters, they are considered to be a sister group of the angelsharks and sawsharks within the squalomorph sharks. The squalomorph sharks, in turn, are the sister group of the galeomorph sharks, a group that includes the horn sharks, carpet and nurse sharks, catsharks, mako sharks and white sharks, and requiem sharks. The squalomorph sharks include the sixgill and sevengill sharks and dogfish sharks in addition to the angelsharks, sawsharks, and skates and rays. These relationships make intuitive sense, because both squalomorph sharks, except for the most primitive members, and skates and rays lack an anal fin. Moreover, both groups are, for the most part, adapted for a benthic existence, and the sequential squalomorph sister taxa of skates and rays, angel- and sawsharks, share many anatomical characters with the skates and rays.

Recent molecular data, however, offer some support for the traditional relationship of skates and rays as a sister group of the sharks. If the molecular data are correct, suggesting that sharks and skates and rays shared a common ancestor, then squalomorph sharks and skates and rays independently acquired their adaptations for benthic habitats. As of 2002 the



Dorsal and ventral views of a female ray, *Raja clavata*. (Illustration by Gillian Harris)

relationships of the skates and rays to the remainder of the cartilaginous fishes remain uncertain. Problems with classification of both the skates and rays and the sharks are due to their geological age and mediocre fossil record and, possibly, their parallel evolutionary trajectories.

As of 2002 the 513 species of skates and rays are classified within 63 genera and 20 families. The families are classified into eight suborders, although the higher-level classification is a work in progress. Most of the species are in the electric ray family Narcinidae (about 30 species), the guitarfish family Rhinobatidae (about 40 species), the skate family Rajidae (about 250 species), the round ray family Urolophidae (about 25 species), the freshwater stingray family Potamotrygonidae (about 25 species), and the stingray family Dasyatidae (about 63 species).

Physical characteristics

Skates and rays share a large number of characters, and as of 2002 there is little doubt that they form a natural group of fishes. They are defined largely by their adaptations for a benthic existence. In fact, they may have the ideal structure among vertebrates for such an existence. All taxa are flattened, at least anteriorly, with the pectoral fins joined to the head and trunk to form a disc. Eyes and spiracles are located on the upper side of the head; the nostrils, mouth, and gill slits are found on the ventral side of the head. Only a few sharks, orectolobids (carpet sharks), and squatinids, but no bony fishes, approach skates and rays in their degree of dorsoventral flattening. Flatfishes (bony fishes) are greatly laterally flattened or compressed, with both eyes on the same side of the head and the mouth contorted slightly to greatly. In other words, to achieve the degree of flatness of skates and rays,

flatfishes had to become asymmetrical. Apparently, sharks and rays have the evolutionary potential to become depressed, whereas bony fishes are morphologically constrained from assuming such a posture.

Many of the distinguishing characteristics of skates and rays are concerned with the structural demands of their depressed shape. The vertebrae between the cranium and the shoulder girdle are fused into a tube (synarchial), the upper cartilage of the shoulder girdle (suprascapula) is either joined or articulated with the vertebral column or synarchial, the anterior pterygium cartilage of the shoulder girdle indirectly or directly joins the side of the cranium, and the upper jaw lacks an articulation with the cranium. All but the last of these adaptations provide the structure to support the expanded disc. The pectoral fin is supported anteriorly by the cranium, medially by the vertebral column, and posteriorly by the trunk, and this support system has allowed massive pectoral fins to develop in the majority of skates and rays. The massive pectoral fins made it possible for these ray fishes to swim by means of undulating or oscillating their pectoral fins. Freeing the upper jaw from the cranium provided greater versatility in feeding both on and in the benthic habitat.

Skates and rays vary in their degrees of flatness and disc development. The more primitive taxa, sawfishes (pristids) and guitarfishes (rhinids, rhinobatids, platyrhinids, and zanobatids), have rather small discs and stout, sharklike tails. These fishes swim by laterally undulating the trunk muscles like the sharks. Electric rays, thought to be the most primitive of the skates and rays, likewise have stout tails but rather expansive discs. They retain a large number of primitive characteristics, however. The large discs house the branchial electric organs that distinguish the group, and large discs may have been independently derived in this group to house the electric organs.

The skates (rajids) and stingrays (plesiobatids, hexatrygonids, urolophids, potamotrygonids, urotrygonids, dasyatids, gymnurids, myliobatids, rhinopterids, and mobulids) have very large, laterally expanded discs and slender to very slender tails. The tails of skates are slender, whereas those of stingrays are slender to very slender and mostly whiplike, and they bear one or more serrated spines. Both skates and stingrays swim by vertically undulating their discs or, in the case of the more derived stingrays, by vertically oscillating the discs like birds in flight. Stingrays have a ball-and-socket connection between the shoulder girdle and the vertebral column and an extra synarchial behind the shoulder girdle. Some of the derived forms of stingrays can generate enough speed to leap clear of the water. Skates lack the ball-and-socket connection, but they have bilobed pelvic fins with a finger-like anterior lobe. The anterior lobe can be used to "walk" or "punt" along the bottom. Punting is a unique locomotive gait of skates.

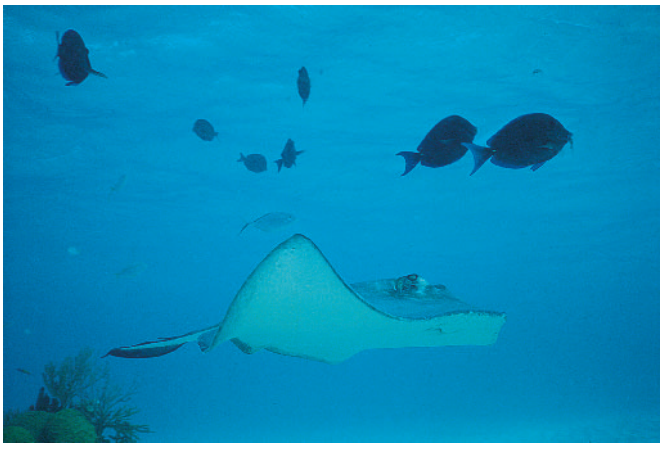
The arrangement of the eyes on the upper surface and the mouth on the lower surface means that skates and rays are unable to see their prey except at a distance. In fact, vision may play only a secondary role in feeding. Like sharks and some bony fishes, skates and rays have electric organs, ampullae of Lorenzini, symmetrically arranged around their mouths. The ampullae are at the end of pores and tubes filled with a conductive substance and are capable of responding to small electric currents, such as those produced by the muscle contractions of prey organisms. Skates and rays also have closed lateral line systems on the ventral surface that are sensitive to small jets of water pressure, such as those produced by bivalve mollusks that are often the prey of these fishes. When a jet of water strikes the surface in the vicinity of the canal system, it causes the fluid in the canal system to flow. Sensory cells lining the canal system perceive the moving current.

Two nostril-like features flank the mouth of a skate to guide it to food. The skate's mouth is lined with teeth capable of crushing small snails and crustaceans. (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

Members of two suborders, electric rays and skates, produce electric currents by means of modified muscle cells. Some of the gill arch or branchial muscles of electric rays are modified into electric cells that can produce up to 200 volts. These cells occupy most of the lateral area of the disc and are used to stun prey and defend against predation. Some electric rays have an auxiliary electric organ behind the main one that produces weak electric currents that may be used for communication among members of a population. Discharges of one individual can be perceived by the ampullae of Lorenzini of another individual. Skates have weak electric organs along the sides of the tail that apparently are used in communication among members of a population.

Skates and rays vary considerably in body size. Some electric rays (Narcinidae) mature at about 4 in (10 cm) in total length. Some skates (Rajidae) mature at about 6 in (15 cm) in total length and are probably the lightest of the chondrichthyans because of their very slender tails and thin discs. Sawfishes, on the other hand, can reach up to 23 ft (7 m) in length and have tooth-bearing rostra almost 6.6 ft (2 m) long. Manta rays (*Manta*) can reach 22 ft (6.7 m) in width and have been reported to be up to 29.8 ft (9.1 m) in width.

The coloration of skates and rays appears to be related largely to camouflage. Species that occur in shallow water tend to be dark yellow-brown, various shades of gray, or brown to black dorsally and cream to white ventrally. Those in mucky waters tend to be unpatterned dorsally, whereas those in clear water often are patterned with wavy lines,



A southern stingray (*Dasyatis americana*) with doctorfish (*Acanthurus chirurgus*) near Grand Cayman. (Photo by Charles V. Angelo/Photo Researchers, Inc. Reproduced by permission.)

stripes, bars, or ocelli. The patterning apparently functions in obscuring their outline and thus aids in making them unrecognizable to potential predators. There is little if any sexual dichromism. Species in deep water are typically dark colored dorsally and ventrally.

Distribution

Skates and rays are found worldwide in the marine environment from the shoreline to about 9,842 ft (3,000 m) and in many tropical freshwaters. The greatest diversity of species to subordinal taxa is in the tropical Indo-West Pacific, although not all of the higher taxa are represented in this region. The Indo-West Pacific region includes the tropical waters from the east coast of Africa to the east coast of Australia and Japan. With the exception of the stingrays, rajiforms are almost entirely absent from the coral islands of the central and western Pacific.

With few exceptions electric rays are limited to tropical and warm temperate seas over continental shelves. Torpeninid electric rays range into temperate latitudes, and some narcinid electric rays (*Benthobatis*) occur to depths of about 3,281 ft (1,000 m). Their eyes are minute and covered with skin, suggesting that they are either blind or respond only to light. Narkid and hypnid electric rays are limited to the tropical waters of the Indo-West Pacific.

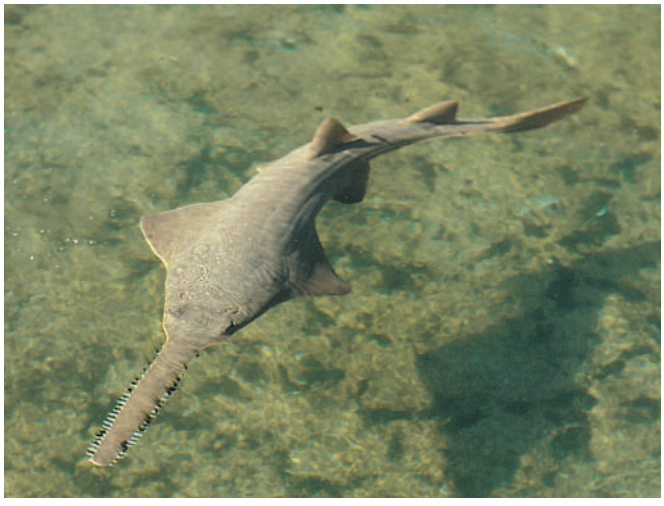
Sawfishes are tropical and apparently limited to coastal, brackish, and freshwaters. Guitarfishes are tropical to warm temperate in coastal and brackish waters. One of the families is limited to the tropical Indo-West Pacific, and the other three families are most diverse in this region.

Skates (rajids) and stingrays (myliobatoids) largely have complementary distributions. In tropical waters skates are absent on inner continental shelves but are abundant in deeper water and in both the north and the south of tropical-subtropical regions. Stingrays, on the other hand, are limited primarily to shallow tropical seas. The stingray families Plesiobatidae (with one species) and Hexatrygonidae (with one to five species) are exceptions and occur to depths of 1,640–3,281 ft (500–1,000 m) under tropical seas. Skates are the only rajiforms that occur at polar latitudes and that are common at great depths, to about 9,842 ft (3,000 m). Few species are found in estuaries, and only one species occurs in freshwater (*Dipturus* sp. from Bathurst Harbour, near Port Davey, Tasmania). Stingrays, on the other hand, are abundant in low-salinity regions, and a number are found strictly in tropical freshwaters. The stingray family Potamotrygonidae is limited to the freshwaters of South America.

Habitat

The majority skates and rays are benthic in marine habitats. The more sharklike forms, such as the sawfishes and guitarfishes, rest on the bottom and swim immediately over the bottom. The more depressed forms, such as the electric rays, skates, and most of the stingrays, rest and swim close to the bottom and often partially bury themselves in the bottom. They undulate their greatly expanded discs while lying over soft substrates to cover themselves partially. When partially covered with sediment, skates and rays ventilate by bringing water in through their spiracles and expelling the water through their gill slits. One species of Dasyatidae (the pelagic stingray, or *Pteroplatytrygon violacea*), the Myliobatidae (eagle rays), Rhinopteridae (cownose rays), and Mobulidae (manta rays) are largely pelagic or at least capable of sustained swimming. *Pteroplatytrygon violacea* and the mobulids spend most of their time and feed in the water column and are at least partially oceanic. The mobulids, however, appear to feed near continents, where upwelling of currents leads to high concentration of zooplankton. Myliobatidae are capable of leaping from the water like the mobulids, but they feed on the bottom.

As a group, chondrichthyans are uncommon in freshwater. Their absence in freshwater is related at least in part to



A smalltooth sawfish (*Pristis pectinata*) swims in the Atlantic Ocean. (Photo by Tom McHugh/Sea World/Photo Researchers, Inc. Reproduced by permission.)

The blue-spotted stingray (*Taeniura lymma*) is widespread in tropical coral reefs of the Indian and Pacific Oceans. (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

the retention of urea in their tissues. Urea acts as a salt and makes chondrichthyans about as salty as seawater. This reduces the costs of osmoregulation in marine waters but increases its costs in freshwaters. Chondrichthyans that enter freshwater apparently have the ability to reduce the urea content in their tissues. The ability to inhabit freshwater is more widespread among skates and rays than sharks. All species of sawfishes and many species of stingrays either move back and forth between saltwater and freshwater or reside permanently in freshwater. Some sawfishes become more freshwater tolerant with age. Numerous dasyatid stingrays move in and out of freshwater. Some dasyatid stingrays reside in freshwater, and the stingray family Potamotrygonidae is limited to the freshwaters of South America. In fact, the potamotrygonids have lost the ability to conserve urea.

Behavior

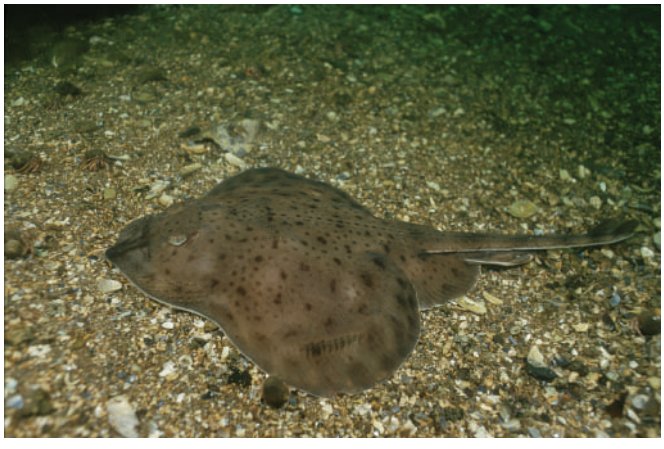
The majority of skates and rays are rather docile, both on a daily basis and over long periods of time. Some of the electric rays and stingrays that live in shallow water may limit daily excursions to moving in and out with the tide. During high tide they move shoreward and burrow into sandy bottoms; at low tide they abandon these depressions and construct similar abodes in deeper water. Limited data from tagging studies suggest that skates are rather provincial. Templeman found that most specimens of a particular skate (*Amblyraja radiata*) tagged off Newfoundland were recaptured within 60 mi (97 km) up to 20 years from the time that they were tagged. In temperate regions benthic species of skates and rays move northward and southward with vernal warming and cooling. More active species, such as eagle rays, cownose rays, and mantas, may be wide ranging, although there are reports that individuals of *Manta birostris* return to the same feeding areas on a yearly basis.

The social behavior and communication of rajiforms are poorly known, but some observations suggest that skates use electrical discharges of their tail electric organs for communication. The organs discharge posteriorly, and males follow directly behind females during mating. All skates have weak electric organs, and the histologic characteristics of the electric cells vary among species. It is thus possible that different species have distinctive electric discharges and that these differences may be used as mate-recognition systems to aid in seeking mates of the same species. Such systems are well known for elephantnose fishes.

Little is known concerning the social relationships between skates and rays and other organisms. There are numerous observations, however, that *Manta birostris* enter shallow water reef areas to be cleaned of ectoparasites by cleaning bony fishes. One species of remora often hitches a ride on *Manta birostris* and even enters the ray's cloaca for extended periods of time. The remora probably feeds on ectoparasites and possibly on the ray's feces.

Feeding ecology and diet

The majority of skates and rays can be considered generalist benthic predators that feed on the more abundant benthic invertebrates and small to moderately sized bony fishes. Some groups, such as the electric rays and sawfishes, have specialized devices for capturing food. The branchial electric organs of electric rays are used to stun fishes and invertebrates, which then are quickly swallowed. Sawfishes use their tooth-bearing rostral blades to disable schooling fishes and to dislodge invertebrates from the substrate. Myliobatid and rhinopterid stingrays have jaw teeth that are fused into crushing plates that enable these fishes to crush bivalve clams, oysters, and mussels. Mobulids have specialized lateral extensions of their rostra (cephalic fins); large, oval-shaped mouths; and filter plates running between their gill arches that allow them to strain zooplankton from the water column. The cephalic fins direct the zooplankton into the mouth, and the filter plates separate the zooplankton from the water that flows over the gill slits. The ampullae of Lorenzini and the closed lateral line systems of skates and stingrays permit these fishes to sense infaunal organisms that can be sucked out of the substratum by means of their protrusible jaws and the sucking action of the mouth and gill cavities.



Winter skate (*Raja ocellata*) on the ocean bottom in the Gulf of Maine. (Photo by Andrew J. Martinez/The National Audubon Society Collection/Photo Researchers, Inc. Reproduced by permission.)

A mermaid's purse skate (*Raja binoculata*) egg sack with live embryos. (Photo by Animals Animals ©Joanne Huemoeller. Reproduced by permission.)

Skates and rays are preyed upon by sharks, and small skates and rays, including egg capsules of skates, are occasionally consumed by large skates and rays.

Reproductive biology

Mating has not been observed frequently in rajiforms, but all species practice internal fertilization. Males possess extensions of their pelvic fin cartilages (claspers) that are inserted into the cloaca of females and serve to transmit sperm into the oviduct. Only one of the pair of claspers is inserted at a time. Generally, copulation occurs between a single male and a single female. In many cases the males bite the anterior margin of the female's disc, to enable them to insert the clasper. Males of many taxa of skates and stingrays have sharp, pointed teeth, unlike the flat teeth of females; these teeth enable the males to remain in contact during copulation. Skates also have sharp, pointed and often barbed, clawlike thorns near the outer corners of their discs, which are used as additional points of contact during copulation.

Fertilization takes place in the anterior section of the oviduct of the female, and the fertilized egg then is encapsulated in the oviductal gland. The encapsulated egg descends into the uterus; in most rajiforms the egg is retained in the uterus, and development is termed "viviparity without a placenta," also termed ovoviviparity. The egg capsules are generally thin, and the embryos may be encapsulated only during the early stages of development. In addition to the yolk supplied with the encapsulated eggs, nutrients are available to the embryos from the uterine wall of the female. Internal development extends from several months to nearly a year among the various taxa of rajiforms. The young or neonates are immature copies of the adults at birth, and the mother provides no parental care.

In skates the encapsulated egg is shed to the environment, and development is termed "oviparity." As with the other rajiforms, the egg is fertilized and encapsulated in the oviductal gland, but the egg capsule is thick, collagenous, and rectangular shaped, with a horn at each corner. The young remain in the capsule from several months to more than a year. Females do not offer any protection for the egg capsules, but it is possible that they seek special areas in which to release them.

Conservation status

Skates and rays have long been exploited by artisanal fisheries and small-scale fisheries in developing countries, but they have not been targeted by large-scale fisheries. Despite the lack of directed fisheries, humans have had a negative impact on populations of many species over the past half-century. Slow growth rates and low reproductive potentials make chondrichthyans, including skates and rays, vulnerable even to modest rates of exploitation. Chondrichthyans have much lower growth rates and fecundity than bony fishes. Thus a fishery directed at bony fishes may inadvertently negatively affect skates and rays before the fishery overexploits the targeted bony fishes. Inshore tropical habitats occupied by many skates and rays have been degraded by human activities, and commercial shrimp fishing has accidentally captured inshore species, such as guitarfishes and sawfishes. Bottom trawling (for shrimps, for example) unintentionally captures large quantities of skates and rays.

As of 2002 the IUCN listed 26 skates and rays as Vulnerable, Endangered, or Critically Endangered. These are species of sawfishes, guitarfishes, skates, or stingrays, and they occupy tropical freshwaters, inshore tropical waters, or continental shelf habitats in temperate regions that are under heavy fishing pressure. All seven species of sawfishes are listed as Endangered (5 species) or Critically Endangered (2 species). Two guitarfishes are listed as either Vulnerable or Critically Endangered. A total of six skates are listed as Near Threatened/Lower Risk (3 species), Vulnerable (1 species), or Endangered (2 species). Eleven stingrays are listed as Near Threatened/Lower Risk (1 species), Vulnerable (4 species), Endangered (5 species), or Critically Endangered (1 species). The Thailand population of *Himantura chaophraya* is Critically Endangered.

Significance to humans

For the most part, skates and rays are not considered high-quality food items. They do enter artisanal fisheries, however, and are landed by numerous commercial fisheries in the Far East and in Europe. Skates and rays are consumed fresh, dried, or salted.

The skin of skates and rays is very tough and can be used as leather. Handles of samurai swords may be covered with guitarfish skin. Various ethnic groups of the Indo-West Pacific once used the teeth of sawfishes and the serrated spines of stingrays as war clubs. Native Americans of the Amazon and Orinoco River drainages capture freshwater stingrays for food and use their serrated spines for arrowheads or as implements for self-mutilation. Today, dried, mutilated skates and rays are sold in seashore curiosity shops.

With the exception of stingrays and large electric rays, rajiforms are not harmful to humans. Bethnic stingrays, , often

lie partially buried in the sand along beaches frequented by human bathers. Bathers who are unfortunate enough to step on a partially buried ray may receive a nasty wound and poison from a gland associated with the spine. This gland at the base of the spine releases neurotoxins and proteolytic toxins.

Some stingrays have contributed to the ecotourism industry. Tourists visit Stingray City in the Cayman Islands to feed large stingrays (*Dasyatis americana*). Scuba expeditions are conducted in Hawaii, the northern Gulf of Mexico, and various other areas, to observe manta rays at their feeding sites.

1. Atlantic guitarfish (*Rhinobatos lentiginosus*); 2. Atlantic torpedo (*Torpedo nobiliana*); 3. Roughtail stingray (*Dasyatis centroura*); 4. Smalltooth sawfish (*Pristis pectinata*); 5. Clearnose skate (*Raja eglanteria*); 6. Freshwater stingray (*Paratrygon aiereba*). (Illustration by Gillian Harris)

1. Yellow stingray (*Urobatis jamaicensis*); 2. Spotted eagle ray (*Aetobatus narinari*); 3. Spiny butterfly ray (*Gymnura altavela*); 4. Atlantic manta (*Manta birostris*); 5. Lesser electric ray (*Narcine bancrofti*). (Illustration by Gillian Harris)

Species accounts

Roughtail stingray
Dasyatis centroura

FAMILY
Dasyatidae

TAXONOMY
Raja centroura Mitchill, 1815, Long Island coast, New York.

OTHER COMMON NAMES
French: Pastenague épineuse; Italian: Trigone spinoso.

PHYSICAL CHARACTERISTICS
Size 83 in (210 cm) in disc width as an adult and 13–15 in (34–37 cm) in disc width at birth. The head, pectoral fins, and trunk are flattened and joined to form a broad, rectilinear disc. The disc is about as broad as it is long, and the outer corners are subangular. Tail 2.4 to 26 times the disc length, slender, and whiplike. It lacks a fleshy dorsal keel and dorsal fins, and the caudal fin but has one or more serrated spines and a low ventral fold. Snout moderately long and very obtuse. Mouth moderately wide and moderately arched. Specimens larger than 20 in (50 cm) in disc width have large tubercles or bucklers along the midline and central area of the disc and along the upper surface of the tail. Coloring brown to olive dorsally and white to whitish ventrally.

DISTRIBUTION
Tropical to warm temperate regions in the Atlantic. Ranges from Massachusetts to the northern Gulf of Mexico and Uruguay in the western Atlantic and from the Bay of Biscay to Angola, including the Mediterranean and Madeira.

HABITAT
Benthic habitats on soft bottoms from near shore to about 899 ft (274 m) in the western Atlantic and to about 197 ft (60 m) in the eastern Atlantic.

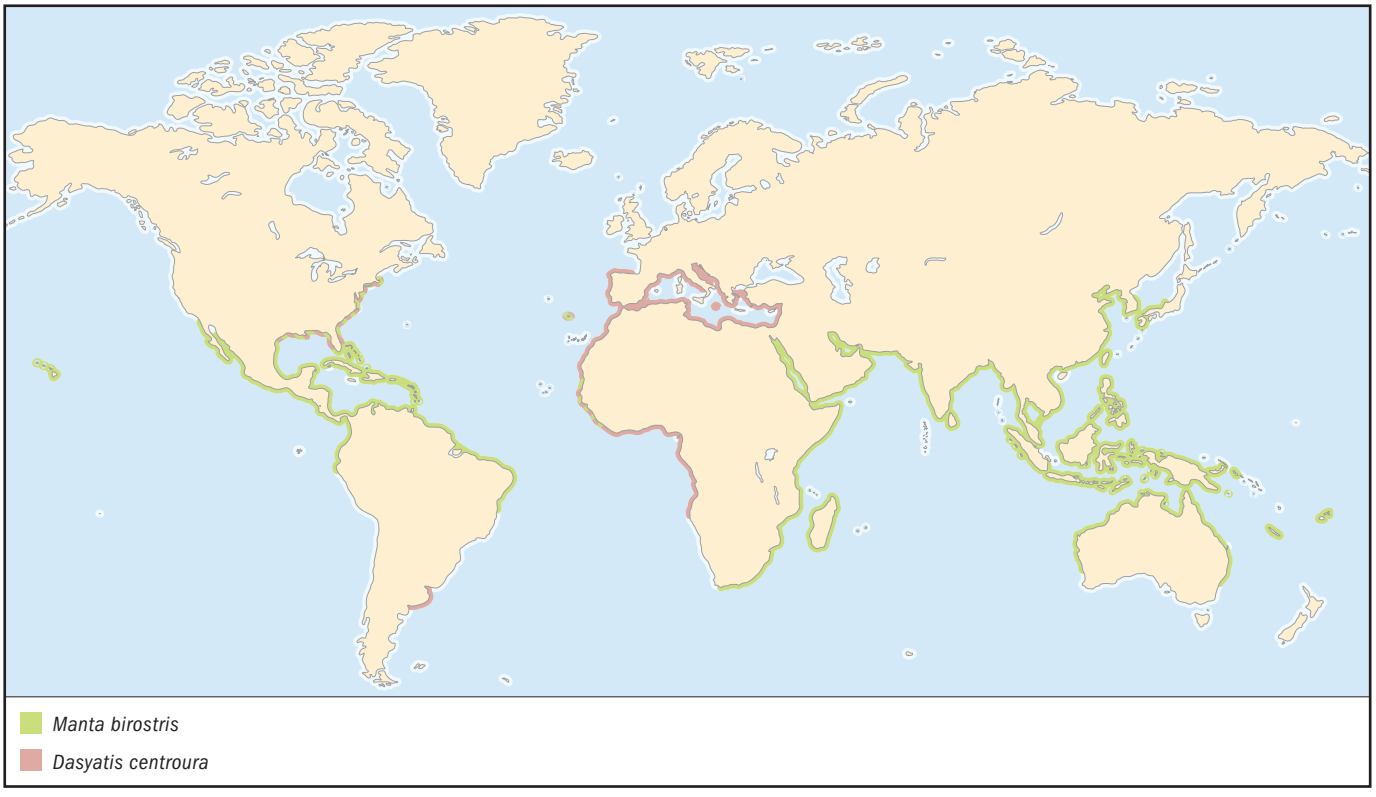
BEHAVIOR
Moves northward and shoreward in the spring and southward and offshore in the autumn.

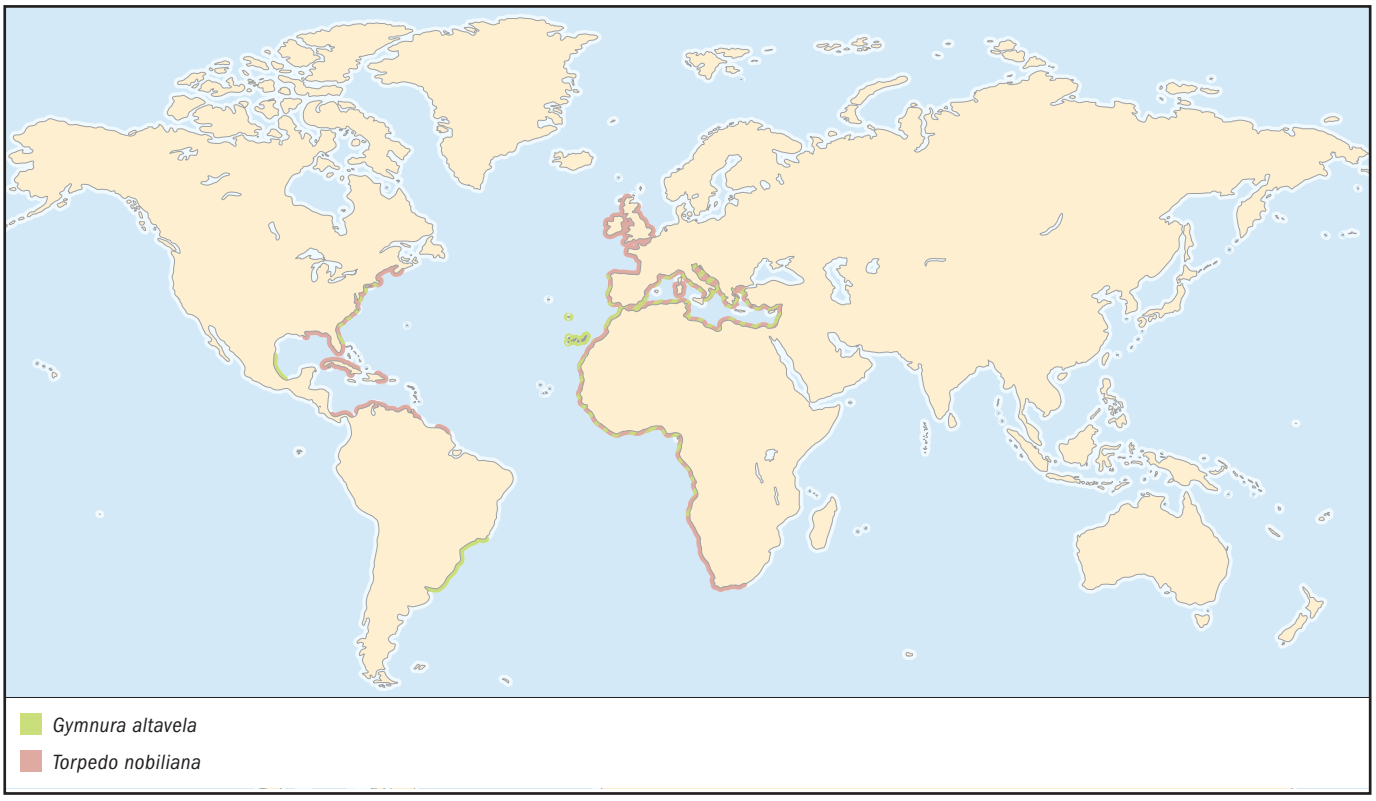
FEEDING ECOLOGY AND DIET
Prey include polychaetes, cephalopods, crustaceans, and bony fishes.

REPRODUCTIVE BIOLOGY
Viviparous, with litters ranging from two to six neonates.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Capable of inflicting painful wounds in waders and swimmers that come into contact with them in inshore areas. ◆





Spiny butterfly ray
Gymnura altavela

FAMILY
Gymnuridae

TAXONOMY
Raja altavela Linnaeus, 1758, Mediterranean Sea.

OTHER COMMON NAMES
French: Raie-papillon épineuse; Spanish: Raya mariposa.

PHYSICAL CHARACTERISTICS
Size 80 in (202 cm) in disc width. The head, pectoral fin, and trunk are flattened and joined to form a very broad rectilinear disc. Disc 1.5 times broader than it is long, and the outer corners are abruptly rounded. Tail very short and slender, about one-fourth of the disc width. It lacks dorsal and caudal fins but has one or more serrated spines and dorsal and ventral ridges. Snout short and very obtuse. Mouth moderately arched. There is a tentacle-like structure on the inner posterior margin of the spiracle. The body is naked, except for small denticles over central areas of the disc. Coloring dark brown and white ventrally. Dorsal surface patterned with small dark and light spots.

DISTRIBUTION
Tropical to warm temperate waters of the Atlantic. Ranges from southern Massachusetts to Rio de la Plata, Argentina, in the western Atlantic and from Portugal to Angola, including Madeira, the Canary Islands, and the Mediterranean Sea, in the eastern Atlantic.

HABITAT
Benthic habitats on soft bottoms from near shore to about 197 ft (60 m).

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
Prey include mollusks, crustaceans, and bony fishes.

REPRODUCTIVE BIOLOGY
Viviparous, with litters ranging from four to seven neonates. The gestation period is about six months.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Capable of inflicting painful wounds in waders and swimmers that come into contact with them in inshore areas. ◆

Atlantic manta
Manta birostris

FAMILY
Mobulidae

TAXONOMY
Raja birostris Walbaum, 1792, type locality not specified.

OTHER COMMON NAMES
English: Giant manta; French: Mante géante; Spanish: Manta voladora.

PHYSICAL CHARACTERISTICS
Size 22 ft (6.7 m) in disc width as an adult and 47 in (120 cm) in disc width at birth. The head, pectoral fin, and trunk is flattened and joined to form a broad rectilinear disc. The disc is

much broader than it is long, and the outer corners are slightly falcate. Tail very short and whiplike. It lacks folds, keels, and a caudal fin but has a dorsal fin at the base and either has or lacks a small serrated spine. The anterior section of the pectoral fin forms a narrow, vertically oriented cephalic fin that is attached to the head and is free of the remainder of the fin. Head slightly elevated and very broad. Mouth is terminal. Teeth are small and located only on the lower jaw. Brown to olive in color dorsally and white to whitish ventrally.

DISTRIBUTION
Tropical to warm temperate regions worldwide.

HABITAT
Pelagic species in near shore to oceanic waters but is most common in coastal waters.

BEHAVIOR
Performs somersaults during feeding. Occasionally leaps partially or completely out of the water. Enters shallow reef areas to be cleaned of ectoparasites by small bony fishes.

FEEDING ECOLOGY AND DIET
Prey include zooplankton and nektonic crustaceans.

REPRODUCTIVE BIOLOGY
Viviparous. Litters size unknown.

CONSERVATION STATUS
Listed by the IUCN as Data Deficient.

SIGNIFICANCE TO HUMANS
Harpooned or gill-netted for human consumption in some parts of the world. It is the focus of underwater scuba-based ecotourism. ◆

Spotted eagle ray
Aetobatus narinari

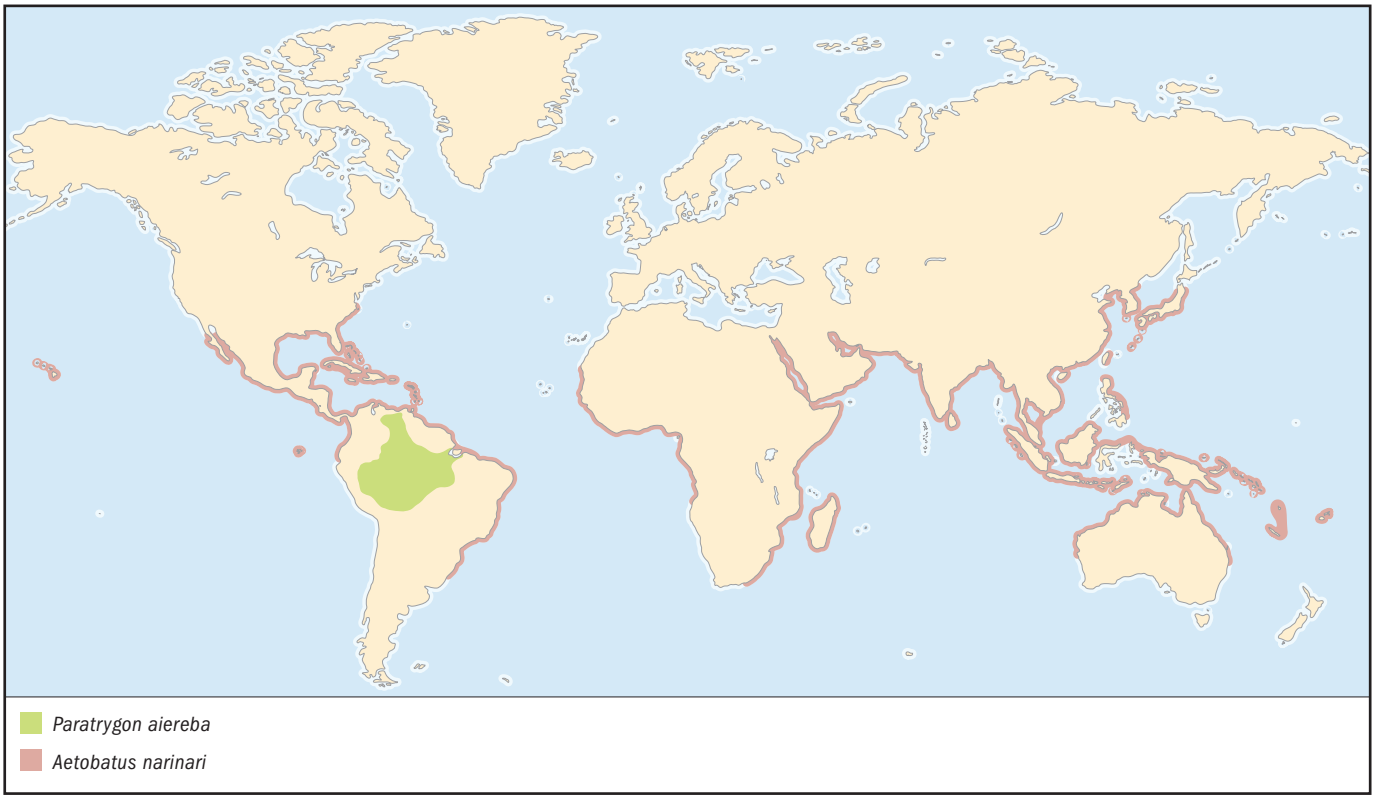
FAMILY
Myliobatidae

TAXONOMY
Raja narinari Euphrasen, 1790, Brazil.

OTHER COMMON NAMES
French: Aigle de mer léopard; Spanish: Chucho pintado.

PHYSICAL CHARACTERISTICS
Size 130 in (330 cm) in disc width as an adult and 7–14 in (18–36 cm) in disc width at birth. The head, pectoral fins, and trunk are flattened and joined to form a broad rectilinear disc. The head is elevated from the disc, and the anterior section of the pectoral fins forms a subrostral lobe above the mouth. Disc 2.1 times broader than long, and outer corners are slightly falcate. Tail very long, slender, and whiplike. It lacks folds, keels, and a caudal fin, but it has a dorsal fin at the base and one or more serrated spines. Snout moderately short; mouth is straight. Teeth flattened and pavement-like and aligned in series. The body is naked. Color ranges from olivaceous to dark brown dorsally and white ventrally, except for a dusky subrostral line and dusky pelvic fins. The dorsal surface is patterned with small white, greenish, or yellow spots.

DISTRIBUTION
Tropical to warm temperate regions worldwide. Species may represent a series of cryptic species, each limited to a particular location. It ranges from North Carolina to southern Brazil, including the Gulf of Mexico in the western Atlantic, Cape Verde to Angola in the eastern Atlantic, the entire tropical and subtropical region of the eastern Pacific, and throughout the tropical and subtropical Indo-West Pacific.



HABITAT
Benthic. Occurs from near shore to about 197 ft (60 m).

BEHAVIOR
Spends much of its time actively swimming in the water column by the oscillatory action of its pectoral fins. It is capable of leaping clear of the water.

FEEDING ECOLOGY AND DIET
Prey include shellfish, such as clams, oyster, whelks, and other mollusks.

REPRODUCTIVE BIOLOGY
Viviparous, with litters ranging up to four neonates.

CONSERVATION STATUS
Listed by IUCN as Data Deficient. There is a possibility that future research may reveal that threatened classification is appropriate, but currently information is not sufficient to list the species.

SIGNIFICANCE TO HUMANS
Capable of inflicting painful wounds in waders and swimmers that come into contact with it in inshore areas. Occasionally, it is captured by gill net fisheries for human consumption. ◆

Lesser electric ray
Narcine bancrofti

FAMILY
Narcinidae

TAXONOMY
Torpedo bancrofti Griffith, 1834, Jamaica.

OTHER COMMON NAMES
Spanish: Raya eléctrica torpedo.

PHYSICAL CHARACTERISTICS
Adults up to 23 in (58 cm) in total length but only 3.5–3.9 in (9–10 cm) in total length at birth. The head, pectoral fins, and trunk are flattened and joined to form a fleshy disc. Tail is stout, and the caudal fin well developed. Snout is very blunt, with a narrow, greatly protrusible mouth that forms a short tube. Kidney-shaped electric organs are located on either side of head, giving the skin surface a honeycomb appearance. Coloring yellowish brown to grayish brown or dark brown dorsally and white to creamy white ventrally. The dorsal surface is patterned with dark blotches, spots, and crossbars.

DISTRIBUTION
Tropical to warm temperate waters of the western Atlantic. Ranges from North Carolina to Venezuela, including the northern and western Gulf of Mexico, the Greater and Lesser Antilles, Yucatan, Belize and northern South America.

HABITAT
Benthic habitats on soft bottoms in shallow water.

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
Electric organs are used to stun prey, which consist of polychaetes, other invertebrates, and small fishes.

REPRODUCTIVE BIOLOGY
Viviparous without a placenta. Litter size can be as many as 18 embryos.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Freshwater stingray
Paratrygon aiereba

FAMILY
Potamotrygonidae

TAXONOMY
Trygon aiereba Müller and Henle, 1841, Brazil.

OTHER COMMON NAMES
English: Discus ray.

PHYSICAL CHARACTERISTICS
Size 43 in (110 cm) in disc width. The head, pectoral fin, and trunk are flattened and joined to form an elliptical disc. The disc is longer than it is broad, indented anteriorly, and slightly broader across the anterior third than across the posterior

third. Pelvic fins are covered entirely by the disc. Tail relatively short, broad at the base, and filamentous distally. The preoral snout length is 30–38% of the disc width. The posterior outer margin of the spiracle bears a knoblike process. Eyes small and located just in front of the spiracles. Mouth small; teeth small and few in number. The dorsal surface is covered with small dermal denticles. Light brown dorsally and white ventrally. The dorsal surface is patterned with dark reticular or vermicular blotches.

DISTRIBUTION
Freshwaters of South America from northern Bolivia and eastern Peru to northern Brazil and Venezuela in the Amazon and Orinoco drainages.

HABITAT
Benthic habitats on soft bottoms in rivers.

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
Prey include benthic organisms.

REPRODUCTIVE BIOLOGY
Viviparous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Capable of inflicting very painful wounds in waders and swimmers that come into contact with it. ◆

Smalltooth sawfish
Pristis pectinata

FAMILY
Pristidae

TAXONOMY
Prisitis pectinata Latham, 1794, type locality not specified.

OTHER COMMON NAMES
French: Poisson scie tident; Spanish: Pejepeine.

PHYSICAL CHARACTERISTICS
Reaches 217 in (550 cm) in total length as an adult but only 24 in (60 cm) in total length at birth. Body elongated and moderately depressed, and the snout is prolonged into a long, narrow, flattened blade bearing 24 to 32 pairs of teeth. The blade is about 25% of the total length. The caudal fin is without a distinct ventral lobe. Color dark brownish gray dorsally and grayish white ventrally.

DISTRIBUTION
Tropical to warm temperate western Atlantic from New York to central Brazil, including the Gulf of Mexico, the Caribbean Sea, and Bermuda. It has been recorded from the eastern Atlantic, Mediterranean Sea, the eastern Pacific, Indian Ocean, and the Indo-Pacific region but these records need to be verified.

HABITAT
Lives near shore in bays, estuaries, and freshwater.

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
The blade is used to dislodge invertebrates and to disable fishes.

REPRODUCTIVE BIOLOGY
Viviparous without a placenta. Litters range from 15 to 20 young.

CONSERVATION STATUS
Listed as Endangered by the IUCN. It is protected in Florida and Louisiana state waters.

SIGNIFICANCE TO HUMANS
None known. ◆

Atlantic torpedo
Torpedo nobiliana

FAMILY
Torpedinidae

TAXONOMY
Torpedo nobiliana Bonaparte, 1835, Italy, iconograph.

OTHER COMMON NAMES
French: Torpille noire; Spanish: Tremolina nigra.

PHYSICAL CHARACTERISTICS
Reaches 71 in (180 cm) in total length in adulthood, and 7.9–9.8 in (20–25 cm) in total length at birth. The head, pectoral fin, and trunk are flattened and joined to form a fleshy disc. The tail is stout, and the caudal fin is well developed. The species has a very blunt snout, with a wide and slightly protrusible mouth. Kidney-shaped electric organs are located on either side of the head, giving the skin surface a honeycomb appearance. Coloring varies from brown to purplish brown dorsally and is white with a dark margin ventrally.

DISTRIBUTION
Tropical to temperate waters of the North Atlantic. Ranges from southern Nova Scotia to Venezuela, including the northern Gulf of Mexico, Cuba, and Trinidad in the western Atlantic and the British Isles and Mediterranean Sea to South Africa in the eastern Atlantic.

HABITAT
Benthic habitats on soft bottoms from the shoreline to the upper continental slope at 1,739 ft (530 m).

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
Electric organs are used to stun prey, which consist of fishes.

REPRODUCTIVE BIOLOGY
Viviparous without a placenta. The litter size is unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Clearnose skate
Raja eglanteria

FAMILY
Rajidae

TAXONOMY
Raja eglanteria Bosc, 1800, Charleston Bay, South Carolina.

OTHER COMMON NAMES
French: Raie blanc nez; Spanish: Raya hialina.

PHYSICAL CHARACTERISTICS
Reaches 31 in (78.5 cm) in total length; at birth it measures 5–5.7 in (12.5–14.4 cm) in total length. The head, pectoral fins, and trunk are flattened and joined to form broad, spade-shaped disc. Tail moderately slender and makes up about half of the total length. The caudal fin is poorly developed. Snout moderately long and slightly obtuse, and mouth moderately wide and slightly arched. There are medium-size thorns on the head and in a row from the shoulder region to the first dorsal fin and irregular lateral rows located on either side of the tail. The dorsal surface is covered sparsely with dermal denticles. Coloring is brown to gray dorsally and whitish to yellowish ventrally. The dorsal surface is patterned with dark and light spots and transverse and diagonal dark bars.

DISTRIBUTION
Tropical to warm temperate regions of the western North Atlantic, ranging from Massachusetts to the northern Gulf of Mexico.

HABITAT
Benthic. Found on soft bottoms from near shore to about 390 ft (119 m).

BEHAVIOR
In the northern part of its range this species migrates north and inshore in the spring and south and offshore in the autumn.

FEEDING ECOLOGY AND DIET
Prey include polychaetes, amphipods, shrimps, crabs, and bony fishes.

REPRODUCTIVE BIOLOGY
Oviparous; neonates hatch from egg capsules after several months.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Atlantic guitarfish
Rhinobatos lentiginosus

FAMILY
Rhinobatidae

TAXONOMY
Rhinobatus lentiginosus Garman, 1880, Florida.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Reaches 30 in (76 cm) in total length. The head, pectoral fins, and trunk are moderately expanded and joined to form a wedge-shaped disc. Nostril length equals or is slightly longer than the distance between the nostrils. The rostral cartilage of the snout is moderately long and expanded and bears conical tubercles near the tip. Tail stout, and dorsal fins and caudal fin well developed. Caudal fin lacks a distinct ventral lobe. Color gray to olive or dark brown dorsally and white to pale yellow ventrally. The dorsal surface generally is freckled with many small white spots.

DISTRIBUTION
Tropical to warm temperate waters of the western Atlantic and ranges from North Carolina to the southern Gulf of Mexico.

HABITAT
Benthic habitats on soft bottoms from the shoreline to 59 ft (18 m).

BEHAVIOR
Nothing is known concerning the behavior of this species.

FEEDING ECOLOGY AND DIET
Feeds on benthic organisms.

REPRODUCTIVE BIOLOGY
Viviparous without a placenta. The litter size is unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Found in local fish markets in the southern part of its range. ◆

Yellow stingray
Urobatis jamaicensis

FAMILY
Urotrygonidae

TAXONOMY
Raia jamaicensis Cuvier, 1816, Jamaica.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Reaches 28 in (70 cm) in total length. The head, pectoral fin, and trunk are flattened and joined to form an oval-shaped disc. The disc is longer than it is broad, and the outer corners are broadly rounded. Tail stout and relatively short, less than half its total length. It lacks dorsal and ventral folds and keels and dorsal fins but has one or more serrated spines and a small caudal fin. Snout moderately short and rounded; mouth small and straight. The body is naked, except for small denticles along the midbelt of the disc and tail. Green to grayish brown dorsally and yellowish, greenish, and brownish ventrally. The dorsal surface is patterned with fine reticulations or light-colored spots.

DISTRIBUTION
Tropical to warm temperate waters of the western Atlantic, ranging from Cape Lookout, North Carolina, to southern Florida, including the Gulf of Mexico, Bahamas, and Greater and Lesser Antilles.

HABITAT
Benthic. Found on soft bottoms from near shore, including bays and estuaries.

BEHAVIOR
Docile. Spends much of its time partially buried in soft substrates.

FEEDING ECOLOGY AND DIET
Prey include benthic invertebrates and bony fishes.

REPRODUCTIVE BIOLOGY
Viviparous, with litters ranging from two to four neonates.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Capable of inflicting painful wounds in waders and swimmers that come into contact with it in inshore areas.

Resources

Books

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Carroll, Robert L. *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman and Company, 1988.

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Organizations

American Elasmobranch Society, Florida Museum of Natural History. Gainesville, FL 32611 USA. Web site: <http://www.flmnh.ufl.edu/fish/Organizations/aes/aes.htm>

John D. McEachran, PhD

Coelacanthiformes
(Coelacanths)

Class Sarcopterygii
Order Coelacanthiformes
Number of families 1

Photo: Coelacanths (*Latimeria chalumnae*) are known from the fossil record dating back over 360 million years. (Photo by Planet Earth Pictures, Limited. Reproduced by permission.)

Evolution and systematics

The living coelacanths are often celebrated as the most unusual case and important example of animal evolution. The first fossil coelacanths were recognized in rocks between 380 and 75 million years old. More than 100 years ago Woodward published the first review on these fishes. Fossils younger than 75 million years were never found, as if all coelacanths had become extinct at that time, very much like the dinosaurs. The bony structures in these fossil crossopterygians, especially their paired (pectoral and pelvic) fins, placed them close to the ancestor of the first amphibians and all other land vertebrates.

It is of no surprise, therefore, that the December 1938 find of a living coelacanth, when announced to the world by J. L. B. Smith in March 1939, caused disbelief and created one of the greatest biological sensations of the last century. Finding a living coelacanth—morphologically so similar to the fossil specimens left in rocks more than 75 million years ago—was as inconceivable as meeting a living dinosaur on a weekend walk.

The living coelacanth, sometimes known by the common name "gombessa," is a single advanced life form that has survived with relatively little change for nearly 400 million years. While some of the coelacanth's relatives became implicated in the ancestry of all terrestrial vertebrates, the aquatic descendants developed structural solutions to life absent in other animals. For example, instead of the calcified vertebrae that normally reinforce the axial skeleton, the coelacanths evolved a strong-walled elastic tube that is as far transformed from the notochord as are the vertebrae. Instead of a solid braincase, they evolved a two-part neurocranium with an intracranial joint that is operated by a special basicranial muscle. It is the only animal with that structure living today. This intracranial joint and other unique rotational joints in the head together with the rostral organs and the gular reticulate electrosensory system may explain the special suction feeding and head standing behavior observed by Hans Fricke.

In the synthesis of coelacanth evolution by P. Forey, a total of 83 species are recognized to have lived between 380 million years ago in the middle Devonian and 75 million years ago in the Upper Cretaceous. There is no fossil record of coelacanths from the past 75 million years. During that time coelacanths lived and died without leaving fossils. The highest diversity of coelacanths during their geological history was recorded in the Lower Triassic (16 species) and in the Upper Jurassic (8 species). While most fossil remnants were found in marine deposits, many were also found in freshwater deposits, especially in the Upper Carboniferous, Lower Permian, Upper Triassic, Jurassic, and Lower Cretaceous.

The first living coelacanth that came to the attention of scientists was named *Latimeria chalumnae* by J. L. B. Smith in 1939. Upon seeing a second specimen in 1952 and noting that it lacked the first dorsal fin, Smith considered it a new species and named it *Malania anjouanae*. When it was found later that except for the lack of the first dorsal fin all other structures were like the first specimen, it was concluded that this first dorsal fin was probably bitten off by a shark, and *Malania anjouanae* become a synonym of *Latimeria chalumnae*.

A second species of coelacanth, *Latimeria menadoensis*, was discovered near Sulawesi by M. V. Erdmann in 1998.

Scientists examine a coelacanth (*Latimeria chalumnae*) that was caught by a fisherman in Kenya. Until 1938 the coelacanth was thought to have vanished with the dinosaurs 75 million years ago. (Photo by George Mulala/Reuters NewMedia Inc./Corbis. Reproduced by permission.)

At the beginning of the twenty-first century, one family was recognized: Latimeriidae. It contains one genus (*Latimeria*) and two species: *Latimeria chalumnae* and *Latimeria menadoensis*.

Physical characteristics

The living coelacanth is often referred to as a "living fossil." A representative of an ancient group whose other members have all gone extinct, it has survived for millions of years with a virtually unchanged body form. Studies of the living coelacanth's soft anatomy and body fluids have shown various similarities with chondrichthyans. These characteristics are thus considered "primitive vertebrate features," but the coelacanth has also developed many specialized characteristics.

Coelacanths have several unique characteristics, the most obvious of which are the fleshy (lobate or pedunculate) fins. While these fins have some similarity with the lobate fins in fossil lungfishes, rhipidistians, and some polypterids, no other fish group has developed seven fleshy fins. The paired fins are supported by girdles that resemble the purported precursors of the pectoral and pelvic girdles of tetrapods. The axial skeleton of coelacanths evolved differently from that of other vertebrates, even those with a persistent notochord. Instead of developing vertebrae, the notochord of the living coelacanth developed into a tube, over 1.57 in (4 cm) in diameter in adults, which is stiffened by fluid under pressure.

The skull of coelacanths has an intracranial joint that divides the neurocranium into an anterior and a posterior half and that allows the mouth to open not only by lowering the lower jaw but also by raising the upper jaw. This increases the gape considerably, and by extending the buccal cavity creates a strong suction. No other living animal has this feature.

Adult coelacanths have a minute brain (occupying only 1.5% of the cranial cavity) in common with many deep-sea sharks and the sixgill stingray (*Hexatrygon bickelli*). The pineal complex, which is involved with photoreception in many vertebrates, is relatively primitive and undifferentiated in *Latimeria*, whereas the basilar papilla in the inner ear has some similarity to that of tetrapods. The electrosensory systems in the head and the gular plates, in addition to the rostral organs, might be useful for locating prey.

The coelacanth has a spiral valve with unique, extremely elongate, nearly parallel spiral cones in its intestine. The valvular intestine is a shared character with ancestral jawed fishes (Gnathostomata), progressively reduced in actinopterygians and replaced by an elongated intestine in teleosts and tetrapods. The heart is elongate but is not simple; it is as complex as in other fishes, and far removed from the superficial earlier interpretation as an S-shaped embryonic tube. Bogart, Balon, and Bruton reported in 1994 that a *Latimeria chalumnae* specimen caught in April 1991 at Hahaya, Grand Comoro, has a 48-chromosome karyotype. This karyotype is unlike those found in lungfishes but is very similar

to the 46-chromosome karyotype of one of the ancient frogs, *Ascaphus truei*.

The complex dermal canals known only from fossil jawless and jawed fishes are combined in *L. chalumnae* with the common pit lines of superficial neuromasts (lateral line) of extant fishes. Therefore, retention and specialization of ancestral structures, no longer present in other living fishes, is one of the most significant attributes represented, along with their evolutionary persistence, in this true "living fossil."

The coloration of *Latimeria chalumnae* is bluish grey with large whitish marks scattered on the body, head, and the fleshy fin bases. The white markings are specific to each individual, so each single fish can be distinguished. The white marks simulate white sessile tunicates on the walls of caves where coelacanths aggregate and on the substrate over which they drift, so that the animals blend perfectly with their background. On a dying coelacanth the bluish hue turns brown, the color of all dead specimens. The Indonesian coelacanth was brown when still alive with much golden glitter in the whitish markings.

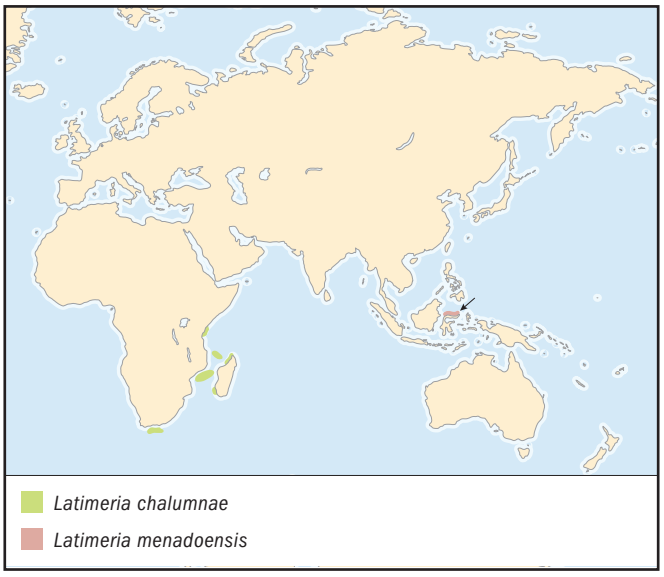
Females grow to 74.8 in (190 cm), males to 59.1 in (150 cm) and 110–198 lb (50–90 kg). Individuals are 13.8–15 in (35–38 cm) long at birth.

Distribution

Since 1998 the coelacanth distribution is known to be not only in the west Indian Ocean, but also 6,214 mi (10,000 km) east on the other side of the Indian Ocean. The specimen that was caught off the Chalumna River in 1938 was later thought to be a stray from the Comoran population around Grand Comoro and Anjouan. Captures near Malindi (Kenya) and at Sodwana Bay near St. Lucia estuary in South Africa extend the range of intermittent distribution along the East African coast. It has not yet been established whether these are discrete populations. Only the Mozambique specimen and the southwest Madagascar specimens were proven to be of Comoran origin. According to Victor Springer, *Latimeria menadoensis* in Indonesia is most likely isolated from the western population(s) by unsuitable habitats in the central Indian Ocean.

Habitat

The extant coelacanths are tropical marine fishes inhabiting inshore water below 328 ft (100 m) depth. They seem to prefer steep sloping areas with little coral sand deposits. The hemoglobin of *Latimeria chalumnae* has the best affinity to oxygen at 61–64.4°F (16–18°C). This temperature coincides with the isobaths of 328–984 ft (100–300 m) in most localities inhabited by coelacanths. As there seems to be very little prey at these depths, the coelacanth is forced to ascend at night to more shallow waters in order to feed, risking some respiratory discomfort. For the daytime, coelacanths descend back into more comfortable temperatures and hide in groups under overhangs and in caves. A sluggish locomotion and drifting instead of fast active swimming probably help to save energy. If this is the case, then a fish hauled to the surface often with a water temperature far above 68°F (20°C) is under such respiratory stress that its survival is uncertain even if it is released back into cooler waters.



At Grand Comoro most coelacanth catches have occurred over the newest lava flows of the periodically erupting volcano Kartala. These lava fields under water consist of more cavities where prey can hide, and more caves for daytime aggregations of coelacanths than other less steeply sloping shores.

Behavior

Coelacanths aggregate in caves and overhangs about 328–656 ft (100–200 m) deep during the daytime. At Grand Comoro 19 adults were counted in one cave close together, gently moving their paired fins but never touching each other. Individuals distinguished by their specific white markings were found faithful to a particular cave for many months, although every day some strayed into other caves. At night the fish drifted individually close to the substrate.

After the first observations in 1987 from the submersible *GEO*, Hans Fricke noted that at night, all individuals took advantage of up- or down-wellings and drifted slowly with the current. The paired fins stabilized the drifting fish so that "all individuals seemed perfectly oriented in that they avoided obstacles in their environment, apparently detecting them well in advance." Fricke further commented that "all individuals irregularly performed a curious headstand, lasting up to 2 minutes."

During swimming, the coelacanth very slowly moves its paired fleshy pectoral and pelvic fins alternatingly in the manner of a trotting horse (left pectoral and right pelvic simultaneously and then right pectoral and left pelvic together). This pattern is also common to lungfish and a few other bottom-dwelling fishes and, of course, most tetrapods. The unpaired fleshy second dorsal and anal fins are sculled in synchrony from side to side and are the main organs for forward propulsion. This explains their similar shape and exact juxtaposition. The nonfleshy first dorsal fin is usually folded

and flush with the dorsal surface in undisturbed fish, but when spread it appears to be used as a sail and/or for lateral display when the fish feels threatened. The large caudal fin (in fact the third dorsal, epicaudal, and second anal) is held rigid during drift-swimming as in weakly electric fishes (to enable interpretation of the electric field distortions), but provides powerful propulsion during rapid forward bursts. The small epicaudal lobe is bent to and fro when the coelacanth is swimming, drifting, or standing on its head, and may be implicated in electro-reception together with the rostral organ and the reticulate organs. The *GEO* team was able to induce headstands in the coelacanth by emitting weak electric currents from electrodes held in the submersible's remotely controlled arm.

Fin coordination probably developed to stabilize the bulky body of the coelacanth, but could in its extinct ancestors have facilitated the eventual transition to locomotion on land. When coelacanths have been observed coming in contact with the substrate, the paired, fleshy fins were not used for locomotion. The coelacanth probably never walks.

Feeding ecology and diet

Latimeria chalumnae is an opportunistic nocturnal bottom drift feeder. Prey items identified in several studies are benthic or epibenthic dwellers like some lanternfishes, deepwater cardinal fishes, cuttlefishes, snappers, cephalopods, and even a swell shark. Most of these are known to hide in bottom cavities.

The coelacanth prefers fresh lava rocks with cavities not filled by coral sand. Being a sluggish swimmer with a low metabolic rate, it regularly performs intermittent head stands during its nocturnal drifts along the bottom. *Latimeria* is able not only to move its lower jaw but, thanks to the intracranial joint, to lift its upper jaw. This feature, unique among extant vertebrates, allows for a considerable increase in the oral gape. In addition to the rostral organ the fish has a distinct reticular system in the gular bones under the head that probably also functions as an electro-sensory system.

The cranial morphology of *Latimeria chalumnae* suggests that it is a gape-and-suck predator whose anatomical specializations appear to permit it to extract prey from the crannies and cavities where it takes shelter.

Reproductive biology

Until 1975 *Latimeria chalumnae* had been considered to be an egg laying (oviparous) species because a 64.2 in (163 cm) long female caught at Anjouan in 1972 was found containing 19 eggs the size and color of oranges. But then another female, 63 in (160 cm) long, previously caught at Anjouan in 1962, preserved, and kept as an exhibit at the American Museum of Natural History (AMNH), was dissected in 1975. The curators of this museum were persuaded to cut open the specimen in order to sample needed tissue of some inner organs. The curators discovered in the female's oviduct five well-developed embryos, with a length of 11.8–13 in (30–33 cm), each with a large yolk sac. This finding meant that the living coelacanth is a livebearer (viviparous).

Later, John Wourms and Jim Atz studied these embryos and their mother's oviduct in detail and found that the heavily vascularized yolk sac surfaces were in very close contact with the equally densely vascularized oviduct walls, thus forming a simple placentalike structure. It seems, therefore, that in addition to the yolk, the embryos have a second, more direct, way to receive nutrients from the mother. A third way of obtaining nutrients suggested itself when more females were dissected. One 66-in (168-cm) long female contained 59 eggs the size of chicken eggs, another female had 65 eggs, and yet others had 62, 56, and 66 eggs. All these females produced more eggs than their oviduct would be able to accommodate as embryos. While the five embryos from the AMNH female still had large yolk sacs, the 26 fetuses from the female caught near Mozambique were close to term and had only a scar on the belly where the yolk sac once was. Both groups of embryos/fetuses had well-developed alimentary tracts and dentitions. It is thus possible that additional nutrient delivery occurred through the debris from the supernumerary eggs. After all, it is known that in some shark species the fetuses feed on eggs and siblings, so that at the end only one large predator is born. It is possible that such oophagy, as it is called, also occurs in *Latimeria.*

Further studies of these unborn fetuses revealed exceptionally wide gill-cover membranes full of cells capable of absorbing uterine milk (histotrophes) secreted by the oviduct walls. This type of nutrient transfer is known in some fishes. Finally, the carotenoid pigments in the yolk are also implicated in oxygen delivery. While more investigation is needed, it is clear that the coelacanth is a fish with a very advanced and complex style of reproduction. This is not surprising, given that the Jurassic coelacanth *Holophagus gulo* was probably a live-bearer, and the Carboniferous *Rhabdoderma exiguum*, although still oviparous, had eggs of relatively large size.

Circumstantial evidence suggests that the gestation time of the living coelacanth is very long (about 13 months), that the females become mature for the first time when older than 20 years (as in some sturgeons), and that a female does not deliver young every year but several years apart. Scientists do not know how the internal fertilization of a female is achieved and where the young live right after birth and in subsequent years. No young were noticed from the submersibles either drifting or in caves, and only one or two have been collected free swimming.

Conservation status

After the catch of the "second living coelacanth" became known to science in 1952, the Comoro Archipelago (then a French colony) was recognized as the "home" of the coelacanth. Soon, national ownership was declared for all subsequent specimens, and the second one declared stolen from its "rightful" owners. Only the French were allowed to collect them. J. Millot, a spider specialist on Madagascar, moved to Paris and with J. Anthony started detailed anatomical descriptions of the coelacanth. After close to 80 specimens were accumulated, some were used as diplomatic gifts. Eventually, other nationals joined the frenzy of working on the prestigious animal. Several special expeditions converged onto the

Comoros, but luckily the beast could not be caught at will by the methods employed.

The Japanese imported larger fiberglass boats called *japavas* to supplement the small single log dugout outriggers (*galavas*), and built a fishing school on Anjouan in the early 1980s. At the same time, rumor was started that the fluid from the "notochord" tube when ingested prolonged life. Soon, in addition to the demands for coelacanths for museum exhibitions, a black market for fresh or frozen specimens for "medicinal" purposes was started. The price soared to $3,000 or more per fish, especially during the rule of the white mercenary who called himself Colonel Baku.

The first deployment of Fricke's submersible *GEO* and the first sighting of coelacanths in their natural habitat coincided with the urgent need for conservation. The Coelacanth Conservation Council (CCC) was established by Eugene Balon, Mike Bruton, Christine Flegler-Balon, Hans Fricke, and Rafael Plante when they met in Moroni (Grand Comoro), the capital of the Federal Islamic Republic of the Comoros, in 1987. The CCC was inspired by the Desert Fishes Council that led to the most progressive conservation law in the world, the Endangered Species Act of the United States. Within the next two years, members of the CCC managed to have the coelacanth included in Appendix I of CITES.

Subsequent dives by Fricke and his team with the new submersible *JAGO* at Grand Comoro revealed a serious decline in the number of coelacanths in each previously surveyed cave. Thus the initial estimates of the numbers of adults (200–500) became potentially invalid. In spite of the discovery of additional individuals off Sulawesi in 1998 and lately at Sodwana Bay (South Africa), the living coelacanth remains unique and highly vulnerable because of its narrow habitat range and very specialized physiology and life style. Although the 2002 IUCN Red List does not list *Latimeria menadoensis*, it lists *L. chalumnae* as Critically Endangered.

Significance to humans

Before the coelacanth's value for science was recognized in the mid-twentieth century, it was occasionally consumed for its presumed antimalarial properties. Because of its high oil content, the meat tastes foul and rancid and causes severe diarrhea when eaten. Since 1952 its interest to science has remained extremely high.

1. Coelacanth (*Latimeria chalumnae*); 2. Indonesian coelacanth (*Latimeria menadoensis*). (Illustration by Brian Cressman)

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Organizations

South African Coelacanth Conservation and Genome Resource Programme. South African Institute for Aquatic Biodiversity, Somerset Street, Private Bag 1015, Grahamstown, 6140 South Africa. Phone: +27 (0)46 636 1002. Fax: +27 (0)46 622 2403. Web site: <http://www.saiab.ru.ac.za/coelacanth>

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Eugene K. Balon, PhD

Ceratodontiformes
(Australian lungfish)

Class Sarcopterygii
Order Ceratodontiformes
Number of families 1

Photo: An Australian lungfish (*Neoceratodus forsteri*) near Queensland. (Photo by Tom McHugh /Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

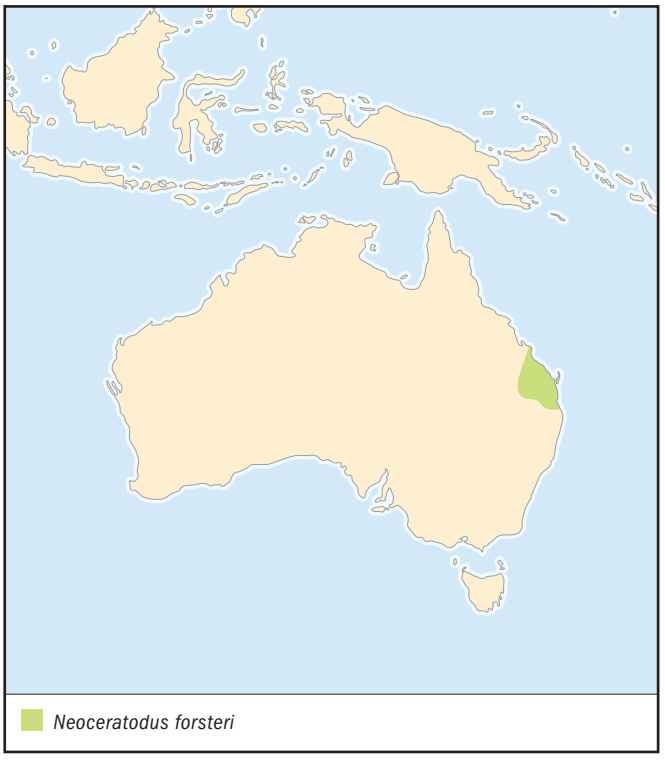
The Australian lungfish is one of the most ancient living species of fishes (indeed, of vertebrates), as fossil remains belonging to *Neoceratodus forsteri* from the early Cretaceous of northern New South Wales are known, giving it a time span of close to 100 million years. The family Ceratodontidae, to which the Australian lungfish belongs, contains other fossil species (known mostly from toothplates), which date from the early Triassic. Many of these fossils, such as those of the genus *Ceratodus*, were more widespread than *Neoceratodus* and occurred circumglobally. *Neoceratodus* is therefore a survivor of a much more successful and ancient lineage. Current opinion diverges in relation to its ancestry, whether it is more closely related to extinct lungfishes of the family Ceratodontidae (the most likely scenario) or to the other living lungfishes of South America (*Lepidosiren*) and Africa (*Protopterus*), in which case *Neoceratodus* would be placed in its own family, Neoceratodontidae.

When first discovered and described by Johann L. G. Krefft in 1870 (as *Ceratodus forsteri*), the Australian lungfish was thought to be an ("gigantic") amphibian, similar to the circumstances surrounding the description of the South American lungfish 33 years before, even though many zoologists regarded *Lepidosiren* as a true "fish" by the mid-nineteenth century. *Neoceratodus* eventually found its place among the Dipnoi, the group containing all lungfishes, both fossil and living (established previously in 1844 by the German zoologist Johannes Müller). The Dipnoi presently contains some 280 fossil species and 60 fossil genera, originating in the early Devonian, in addition to the six species and three genera that are living today. Many of these fossils are known from well-preserved skeletons (some preserved three-dimensionally, such as *Griphognathus* and *Chirodipterus* from Gogo, Australia), but at least half of the species are known only from isolated toothplates. Lungfishes achieved their greatest diversity in the Devonian, when most (if not all) lungfish taxa were marine; living lungfishes are restricted to freshwater.

The systematic position of the Dipnoi among the vertebrates is still being debated. In a landmark study in 1981, Donn E. Rosen and collaborators placed the lungfishes as the closest relatives of the tetrapods (land vertebrates), challenging the widely held belief that certain "rhipidistians" (a heterogeneous group of fossil lobe-finned fishes) were their nearest ancestors. Current views on the ancestry of the tetrapods, based on morphological studies, indicate that lungfishes are their closest relatives if only living taxa are taken into account, but that other extinct groups of lobe-finned, fish-like vertebrates (rhizodonts, osteolepids, *Eusthenopteron*, and "elpistostegids" such as *Panderichthys*) are actually more closely related to tetrapods when all fossil evidence is considered; molecular data bearing on this issue are still controversial. The exclusively Devonian group Porolepiformes, which had pectoral fins anatomically similar to *Neoceratodus*; e.g. *Holoptychius*, is considered by many researchers to be the closest relative of the Dipnoi.

Physical characteristics

Neoceratodus forsteri is morphologically unique, presenting paddle-like or leaf-like pectoral fins that are fleshy and stout at their bases; the pelvic fins are similar, but smaller and not as fleshy as the pectorals. Their heads are wide and slightly depressed, with a terminal mouth. The nostrils are internal, composed of two small openings inside the labial cavity, which are followed by a pair of posterior openings in the roof of the mouth (choanae). The trunk is long and muscular and is laterally compressed, with a protocercal caudal fin that is posteriorly pointed and continuous with both the dorsal and anal fins. Their scales are remarkably large (but rather thin),



overlapping and posteriorly rounded. The teeth are fused into toothplates, two pairs of which are positioned in the roof of the mouth, and one pair on either side of the tongue on the mouth floor; the posterior toothplates are ridged, and in juveniles they are trilobed.

The single lung (a modified swim bladder) is large; highly vascularized and internally divided into two chambers; and connects with the esophagus ventrolaterally. The gills open into a large opercular chamber just ahead of the pectoral fins. Sensory canals of the lateral-line system are visible dorsally on the head and nape (but not as much as in the South American and African lungfishes), and the lateral line runs posteriorly at midheight to the tip of the tail. Large sensory pores are present on the snout and around the eyes. Their skeletons are mostly cartilaginous, in contrast to fossil lungfishes, which were more heavily ossified. Dorsally and laterally, the Australian lungfish is olive to dark greenish brown in color, but ventrally creamy-yellow or even pinkish. Many specimens also have darker blotches dorsolaterally on the tail, especially juveniles.

Distribution

Very restricted in distribution; present only in Queensland, Australia. When the continent was first colonized, this species was already restricted to the Mary and Burnett River systems, but it was subsequently introduced, successfully, into other rivers of southeastern Queensland, such as the Albert, Brisbane, Coomer, Fitzroy and Stanley Rivers, and also in the Enoggera Reservoir, where it is reported to be abundant.

Habitat

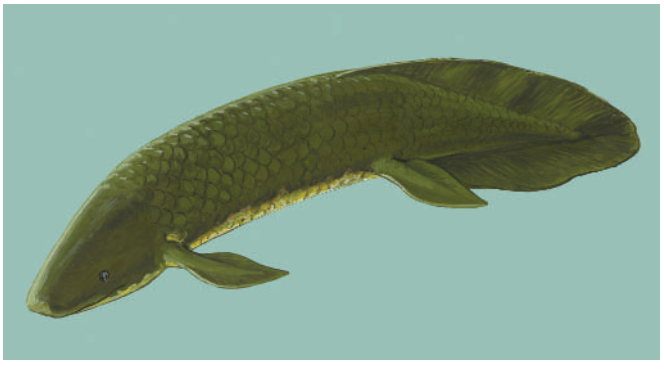
Often found in deep pools in still, slow moving rivers. Its ability to absorb oxygen periodically directly from the air enables it to live in rather stagnant waters. The rivers inhabited by *Neoceratodus* are typically calm and slow moving, with mud, sand, or gravel bottoms, and with plenty of marginal and aquatic vegetation, important for spawning.

Behavior

Mostly sluggish, but capable of quick bursts of speed in pursuit of prey or when threatened. Vision is reportedly poor, as captive specimens have been known to swim into obstacles, but they are known to hunt prey items mostly at night, using electroreception and a refined sense of smell. The single lung allows *Neoceratodus* to breathe air occasionally, but it breathes primarily through its gills and only ascends to the surface to gulp air when water conditions are poor or when the gills are clogged with mud or other debris. In their natural habitat, individuals have been observed to swallow air at intervals of 30 to 60 minutes, emitting a particular sound when air is exhaled. Juveniles and especially hatchlings are also capable of absorbing oxygen through the skin. *Neoceratodus* does not estivate (bury itself in a muddy burrow to wait for the rainy season), as do the South American and African lungfishes, and consequently it cannot remain alive out of water for periods greater than a few days, even if kept wet and in the shade.

Feeding ecology and diet

Essentially carnivorous, eating frogs, other fishes, and invertebrates such as insect larvae, earthworms, snails, and freshwater crustaceans. However, it has also been reported to eat both aquatic and terrestrial plants and even native fruits that have fallen into rivers. Prey items are captured through suction and crushed by the toothplates. The pectoral fins allow them to brace themselves when foraging for prey. Larvae and juveniles of *Neoceratodus* are preyed upon by insect larvae, fishes, and fish-eating birds.



An Australian lungfish (*Neoceratodus forsteri*). (Illustration by Brian Cressman)

The Australian lungfish (*Neoceratodus forsteri*) is also known as the Queensland lungfish, and has changed very little over the past 110 million years. (Photo by Animals Animals ©Fritz Prenzel. Reprodueced by permission.)

Reproductive biology

Reproduction occurs in shallow, warm waters before the summer rainy season. Complex courtship behaviors have been recorded; the pair is not easily distracted. A male and female remain in close association, as the male nudges the cloacal area of the female to stimulate her. Fertilization is external. Spawning may take up to one hour after the pair has chosen a site, usually a patch of aquatic plants. Fifty to 100 sticky eggs are laid on plants, to which they adhere. There is no guarding of the eggs or the young. The eggs are small, spherical, and enveloped by a gelatinous substance. Larvae emerge from the eggs after a period of some three weeks but remain close to them for shelter for some 10 days following. After 41 to 56 days, the yolk disappears and the larvae begin to feed, probably on insect larvae or other small invertebrates. The hatchlings do not have external gills but are capable of breathing air at a very small size, 0.98 in (2.5 cm). A size of 9.8 in (25 cm) is attained after six months, and 19.7 in (50 cm) after 20 months. They resemble adults after approximately six months.

Conservation status

This species is fully protected under CITES (Appendix 2) legislation and cannot be collected without special permit; it is not listed by the IUCN.

Significance to humans

Reported to adapt well to captivity, *Neoceratodus* is common in public aquaria. One specimen lived for more than 50 years in captivity at the Shedd Aquarium in Chicago. It is not consumed. In a more anthropocentric vein, *Neoceratodus*, along with the other living lungfishes and the living coelacanths, *Latimeria chalumnae* and *L. menadoensis*, are of special interest, and are given high profiles in museum exhibits and evolutionary biology textbooks because of their close ancestral ties to land vertebrates, including humans. They are more closely related to tetrapods than they are to the remaining fishes.

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Marcelo Carvalho, PhD

Lepidosireniformes
(Lungfishes)

Class Sarcopterygii
Order Lepidosireniformes
Number of families 2

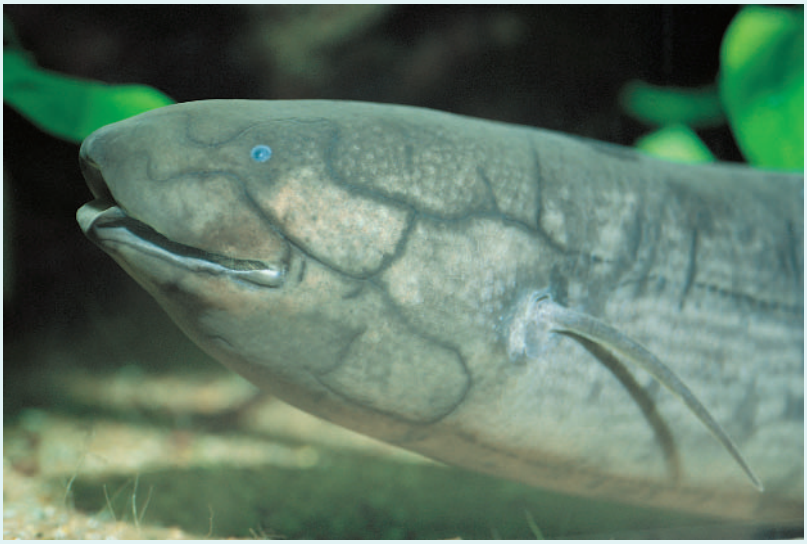


Photo: The South American lungfish (*Lepidosiren paradoxa*) resting in the waters of central South America. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

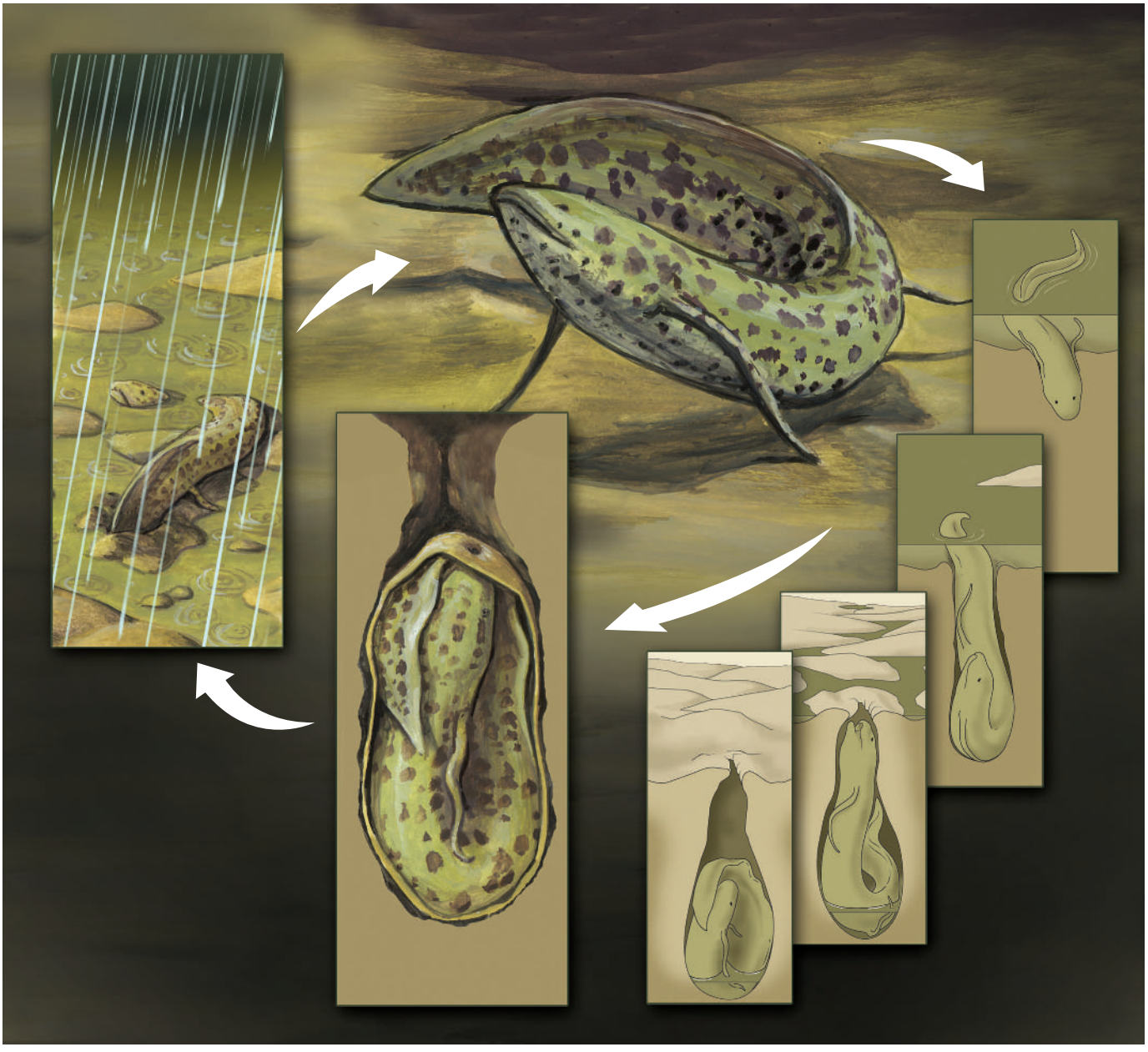
The South American lungfish (*Lepidosiren paradoxa*) was the first lungfish species to be described (in 1837 by Leopold J. F. J. Fitzinger; 1802–1884). It was originally discovered and collected from the Amazon River by Johann Natterer (1787–1843), a dedicated and gifted Austrian naturalist who collected extensively in Brazil from 1817–1835. The first African lungfish was described shortly thereafter in 1839 by the British anatomist Richard Owen (1810–1890), who firmly believed that lungfishes were true "fishes" and not amphibians, mostly on the basis of his erroneous conviction that lungfishes did not have a second (internal) nostril (known as a choana) or a divided auricle. Zoologists of the mid-nineteenth century were divided about the ancestry of lungfishes, wondering whether they were more closely related to amphibians or to other bony fishes. It is now well established that lungfishes belong to a higher group, the Sarcopterygii, which also includes the tetrapods, coelacanths, and many other lobe-finned fossil fishes, and are therefore unequivocally more closely related to land vertebrates than to ray-finned bony fishes (Actinopterygii).

The genus *Lepidosiren* is monotypic, but detailed comparative studies of specimens from most of its extended range are needed (two other nominal species exist, but they are considered synonyms of *L. paradoxa*). Four species of African lungfishes (*Protopterus*) are recognized: *P. annectens*, *P. aethiopicus*, *P. dolloi*, and *P. amphibius*. Some of these species are difficult to distinguish, and are in need of critical taxonomic evaluation, including the validity of certain subspecies (a total of 10 nominal species have been described); their evolutionary relationships to each other have yet to be fully investigated. *Lepidosiren* and *Protopterus* are placed in the same order, but are classified in distinct families. They are closely related to the Australian lungfish (*Neoceratodus forsteri*) and its immediate fossil relatives, while the vast majority of remaining fossil lungfishes are more distantly related (some 60 genera and 280 species and of lungfishes are known). Extant lungfishes are "living fossils," and belong to an ancient lineage, the Dipnoi, that was much more diverse in the Devonian (ca. 417–354 million years ago) and Triassic (ca. 248–205 million years ago) periods. Fossil relatives of *Lepidosiren* and *Protopterus* are known from the late Cretaceous of South America and Africa, respectively, and these genera, along with *Neoceratodus*, are among the oldest vertebrates living today.

Physical characteristics

South American and African lungfishes are morphologically similar, presenting elongated, eel-like bodies, with relatively small heads, and filamentous pectoral and pelvic fins. The pelvic fins are stouter than the pectorals in both genera; the pectorals are slightly more robust in *Protopterus*, and may resemble simple filaments in *Lepidosiren*. The caudal fin is confluent with the dorsal and anal fins (as in the Australian lungfish), tapering distally. The body is compressed laterally, especially at the anus, but not as much as in *Neoceratodus*. The eyes are minute and the mouth is terminal, with a lateral groove extending to the sides of the head. Sensory canals on the head and cheek appear as sinuous, deep lines that extend posteriorly at midbody height towards the tail; sensory pores are also present on the head. The anus is asymmetrical, situated laterally just posterior to the pelvic fins, and not directly in the middle as in *Neoceratodus* (the side may vary among individuals of both *Protopterus* and *Lepidosiren*). The scales are mostly embedded in the skin and are very thin, but clearly visible. The nostrils are on the internal lip margin, and the teeth are fused into sharp tooth plates.

Both *Lepidosiren* and *Protopterus* have two highly vascularized and separated lungs (modified swim bladders), positioned on each side of the gut and connected to the esophagus ven-



Lungfish estivation cycle. (Illustration by Brian Cressman)

trally, as in tetrapods and bichirs (Polypteriformes). The lungs have many alveoli, similar to the lungs of tetrapods. The gill openings are small, not nearly as large as in *Neoceratodus*. Newly hatched individuals have flared external gill filaments, absent in *Neoceratodus*, and these may persist vestigially above the pectoral fins in subadults and adults of *Protopterus*. The skeleton is mostly cartilaginous. Both *Protopterus* and *Lepidosiren* vary slightly in color, from dark brown to deep gray dorsally and laterally, with many varied blotches and spots; usually dark ventrally, although *Protopterus* may be lighter ventrally. *Lepidosiren* may reach 4.1 ft (1.25 m) in length, while *Protopterus* varies from between 17.7 in (45 cm) (*P. amphibius*) to 6.5 ft (2 m) in length (*P. aethiopicus*, which can weigh some 37.5 lb [17 kg]).

Distribution

Lepidosiren has the greatest distribution of any extant lungfish, occurring in many tributaries of the Amazon and Paraná-Paraguay River systems, as well as in French Guiana. Species of *Protopterus* are slightly more restricted. *P. annectens* is present in central and West Africa; *P. aethiopicus* occurs in central and East Africa; *P. dolloi* is restricted to the Congo basin; and *P. amphibius* occurs in coastal East Africa.

Habitat

The South American and African lungfishes are generally found in lentic (slow-moving) rivers, with plenty of associated

vegetation and swampy, stagnant conditions (especially *L. paradoxa*). They can also be found in open lakes (e.g., *P. aethiopicus* in Lake Victoria); floodplains (e.g., *P. dolloi* in the Congo River basin, and *P. annectens* in the Senegal, Gambia, Niger, and Volta Rivers in West Africa); near river deltas (*P. aethiopicus* in Lake Tanganyika, *P. amphibius* in the Zambesi River delta); and in small pools.

Behavior

Lepidosiren and *Protopterus* species are sluggish, swimming through sinuous movements or by "crawling" on their pectoral and pelvic fins, especially to scavenge the bottom. Both genera are obligate air breathers, unlike *Neoceratodus*, which breathes primarily through the gills. *Lepidosiren* and *Protopterus* individuals will drown if forced to stay underwater, as the gill surfaces of these fishes are not large enough to satisfy their oxygen needs. Both genera also employ estivation, being capable of remaining inside a resting chamber for protracted periods during dry seasons and emerging when wet conditions return (estivation has been documented for Permian lungfishes, in the form of fossilized burrows). The degree of estivation varies among the species, but has been particularly well documented for *P. annectens.* The burrows are excavated by biting the soil and expelling mud through the gill openings. The fish will then turn around and remain with its head facing the burrow opening, from where it obtains oxygen. The individual suffers metabolic changes during this period to endure the lack of moisture (detailed below for *P. annectens*). One individual of *P. aethiopicus* remained in its cocoon for four years in captivity. Lungfishes do not feed during estivation. To sustain themselves, they initially metabolize fat reserves and then muscle mass.

Feeding ecology and diet

Lungfishes are mostly carnivorous, feeding mainly on invertebrates (insects, insect larvae, mollusks, crustaceans) but also on fishes and amphibians. Both genera may occasionally feed on aquatic plants. Lungfishes approach potential prey items through ambush or stalking, capturing them by quickly opening their mouths to create negative pressure that pulls them in. Little is known concerning their natural predators, but presumably larger carnivorous fishes and other vertebrates prey on lungfishes, especially when they are juveniles.

Reproductive biology

Spawning is usually seasonal, taking place during the wet season. Fertilization is external. In both genera the adult male guards and aerates the hatchlings and young temporarily. Female *Protopterus* usually lay eggs in burrows excavated by the males. The eggs are small (from 0.16–0.27 in/4–7 mm in diameter), and take one to two weeks to hatch, at which time they resemble tadpoles with slender, featherlike external gills. Only after a period from one month to 55 days do the larvae breathe air. At this stage, they range from 1 in (2.5 cm) to 1.6 in (4 cm) in length, and still have external gills. The larvae remain relatively inactive and are attached to the nest through their cement glands until their yolk reserves have been depleted, at which time they begin to forage for insect larvae and crustaceans and inhale air.

Conservation status

No species of Lepidosireniformes are listed by the IUCN.

Significance to humans

Lungfishes are common in both public and private aquaria. Although they are consumed as food in some parts of Africa, they are not important food fishes. They are harmless, but if provoked can inflict painful bites because of their strong jaws and sharp teeth.

1. African lungfish (*Protopterus annectens*); 2. South American lungfish (*Lepidosiren paradoxa*). (Illustration by Brian Cressman)

Species accounts

South American lungfish
Lepidosiren paradoxa

FAMILY
Lepidosirenidae

TAXONOMY
Lepidosiren paradoxa Fitzinger, 1837, Amazon River; Brazil.

OTHER COMMON NAMES
French: Anguille tété; German: Lurchfische; Portuguese: Pirambóia, peixe pulmonado.

PHYSICAL CHARACTERISTICS
To 4.1 ft (1.25 m) in length. Usually dark brown (sometimes gray) with darker and lighter spots and blotches dorsally and laterally.

DISTRIBUTION
Most of the Amazon basin, from Peru to the Amazon River delta, and in the Paraná-Paraguay Rivers basin as far south as the La Plata system. Recently reported in French Guiana, and probably occurs elsewhere in tropical South America.

HABITAT
Swamps, slow-moving waters, floodplains, and pools.

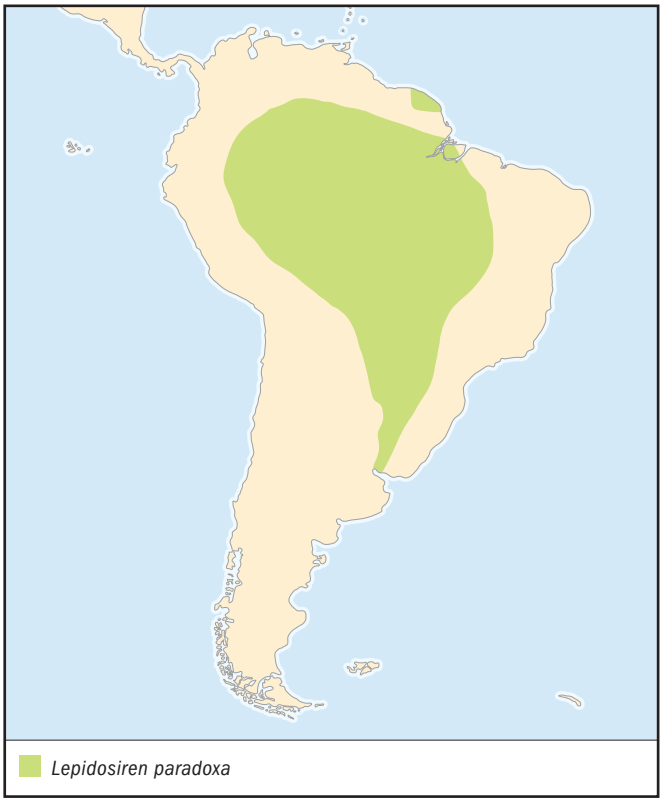
BEHAVIOR
An obligate air breather with reduced gills; can remain inactive for months during estivation, sometimes by closing the chamber opening so as to prevent further desiccation. This species is very intolerant of the close proximity of conspecifics under aquarium conditions. It also may be hyperdispersed in the wild.

FEEDING ECOLOGY AND DIET
Feeds on insects, insect larvae, other invertebrates and fishes, as well as algae; reported to masticate prey before swallowing.

REPRODUCTIVE BIOLOGY
Males present modified pelvic fins during reproduction, which develop featherlike protuberances that are highly vascularized and are believed to be accessory respiration organs, but it is not clear if they aid the adult or the larvae (or both). The male creates burrows in which the eggs are deposited and the larvae develop. Eggs are about 0.27 in (7 mm) in diameter. Hatchlings exhibit four pairs of external gills, and ventral adhesive glands anchor them in the burrow (both gills and adhesive glands are lost after six to eight weeks), after which they emerge to take their first breath of air, at about 1.6 in (4 cm) in length.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Not consumed regularly as food. Often displayed in public aquaria, where it can live for many years. Not widely kept by amateur aquarists and does not figure prominently in the ornamental fish trade. ◆



African lungfish
Protopterus annectens

FAMILY
Protopteridae

TAXONOMY
Lepidosiren annectens Owen, 1839, Congo River. Two subspecies sometimes recognized.

OTHER COMMON NAMES
German: Afrikanischer Lungerfische; Afrikaans: Longvis.

PHYSICAL CHARACTERISTICS
Reaches 3.3 ft (1 m) in length. Separated from other *Protopterus* species by its relatively more slender head; 40–50 scales between operculum and anus, 36–40 scales around body anterior to dorsal fin origin; and 34–37 pairs of ribs. Olive to dark brown dorsally, lighter underneath, usually with spots and blotches on dorsal and lateral aspects.

DISTRIBUTION
Numerous rivers and lakes throughout central, South, and West Africa, e.g., the Senegal, Niger, Gambia, Volta, and Chad basins; the Chari River in Western Sudan; Bandama and Camoé basins in Côte d'Ivoire; Congo basin; the Zambezi and Incomati Rivers in South Africa. Also in Sierra Leone and Guinea, and the upper Nile basin.

HABITAT
Stagnant freshwater habitats, such as swamps and floodplains, also in more flowing rivers and streams.

BEHAVIOR
Estivation is well documented. Individuals will "chew out" a burrow 1.2–9.8 in (30–250 mm) deep, expelling mud through their gill openings. They eventually turn to rest facing the entrance, forming a bulb-shaped chamber that contains water in its lower portion. They periodically extend forward to breathe air from the opening, returning to rest in mucus secreted in the water-filled portion of the chamber. Their metabolic activity decreases progressively as the chamber becomes drier, and the chamber may eventually solidify into a hard cocoon. They may remain for up to seven or eight months in this resting state, until moist conditions return. This species is solitary and hyperdispersed in nature.

FEEDING ECOLOGY AND DIET
Feeds on insects, their larvae, other invertebrates, and fishes, also algae or aquatic plants. May masticate food items repeatedly, and even reported to spit out and intake prey repeatedly during feeding.

REPRODUCTIVE BIOLOGY
Males do not develop vascularized structures on their pelvic fins during breeding. Males usually guard larvae in nest sites that they dig out. Embryos hatch in one to two weeks, with conspicuous external gills, and will become obligate air breathers after about one month.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Kept in public aquaria, and consumed locally but not intensely. Not widely kept by amateur aquarists and does not figure prominently in the ornamental fish trade.

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Marcelo Carvalho, PhD

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Polypteriformes
(Bichirs)

Class Actinopterygii
Order Polypteriformes
Number of families 1

Photo: A Week's bichir (*Polypterus weeksii*) from Congo, West Africa. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Polypteriforms are the most basal or "primitive" living actinopterygian group, according to many recent authors. There are two living genera: *Polypterus* (bichirs), and *Erpetoichthys* (reedfish or ropefish), with 11 to 16 species presently recognized (*Erpetoichthys* has a single species). Their sketchy fossil record suggests that the group has never been particularly diverse. Fossils have been found in both Africa and South America, indicating that they were in existence before the breakup of Gondwana in the early Cretaceous, some 118 million years ago (mya); living forms are restricted to Africa. However, if the most accepted evolutionary scheme is correct, then polypteriforms have been around since much earlier (from at least the late Devonian), as indicated by stratigraphic correlations with fishes more closely related to the remaining actinopterygians (e.g. *Mimia* and *Moythomasia*, from the late Devonian of Australia). The few fossil polypteriform occurrences, usually dermal remains, are from the late Cretaceous (Cenomanian, 100 mya) of Morocco (*Serenoichthys*), Niger (?Campanian, 84 mya) and Bolivia (Maastrichtian, 71 mya), and Paleocene (63 mya) of Bolivia (*Dagetella*). Hence, there is a tremendous gap in our knowledge of polypteriforms, as fossils are as yet unknown from the late Devonian to the Cenomanian, a period spanning some 270 million years. On the other hand, there is molecular evidence suggesting that polypteriforms are more closely related to neopterygians (gars, bowfins, and teleosts), which, if confirmed, slightly reduces the discrepancy with the fossil record.

Uncertainty regarding the evolutionary affinities of polypteriforms is not new, as they have been interpreted as being more closely related to either sarcopterygians or actinopterygians, or even lying somewhere in between (such as in Erik A. Stensiö's Brachiopterygii), at least until the influential 1928 study by Edwin S. Goodrich. Even though the current consensus is to place them among the actinopterygians (following Goodrich), there is much room for refinement. The disagreement over their ancestry stems from their enigmatic amalgam of anatomical features. Some of these features are present in sarcopterygians (lobefins), such as fleshy pectoral fin bases (not the internal pectoral fin skeleton, however), feathery external larval gills, larval cement organs, and paired, vascularized swim-bladders (lungs) arising from a ventral esophageal pneumatic duct; the latter three features are present in lepidosireniform lungfishes and tetrapods. Other features are similar to those present in sharks and rays (e.g., intestinal spiral valve, pectoral fin skeleton). But all of these traits probably evolved independently in the Polypteriformes, which share various derived characters with actinopterygians (e.g., scales with ganoin, dermohyal, gill arch musculature), as summarized by British paleoichthyologist Colin Patterson in 1982. The structure of their eggs (with a single opening for the entry of sperm cells) also supports their evolutionary affinity with actinopterygians.

Evolutionary relationships among polypteriform species, as well as the taxonomic status of many of these (along with their respective subspecies) are in need of further evaluation. Species of *Polypterus* are usually identified by their color pattern and meristics (such as numbers of scales along the lateral line, number of dorsal finlets), but there is overlapping in many features among certain species. Both genera are easily separated, as *Erpetoichthys* lacks pelvic fins and is very elongate, eel-like, with posteriorly positioned, small, and widely separated dorsal finlets.

Physical characteristics

Polypteriforms are morphologically unusual, and as a result their anatomy has been intensely studied over the past 100 years. They are moderately large, ranging from 15.7 to 47.2 in (40 to 120 cm) in total length, and are readily identified,

The bichir (*Polypterus ornatipinnis*) is widespread across Africa. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

presenting a slender body with a depressed head, wide terminal mouth with fleshy lips, and unique, subdivided spiny dorsal fins (finlets). There is a tubular pair of nostrils extending anteriorly beyond the mouth. The teeth are sharp, small, and numerous. The gill opening is large, with an extended skin covering ventrally; four functional gill arches are present. The arrangement of dermal bones of the head and cheek are visible externally. The pectoral fin is greatly rounded posteriorly, with a fleshy base. Each dorsal finlet is composed of a strong, sharp spine attached posteriorly to a dermal fold, which in turn is attached to the base of the succeeding spine. Spines vary from seven to 18 among species, and are bifid (double-edged) at their tips. The dorsal fin originates either shortly after the pectoral fins or farther posteriorly, and is confluent with the caudal fin origin. The caudal fin is posteriorly elongate and distally rounded, composed only of soft rays. Pelvic fins (*Polypterus*) are situated at the posterior third of the body, followed by the anal fin (in both genera) which is very close to the caudal fin (and is functionally correlated with it while swimming); the anal fin, unlike the dorsal fin, is separated from the caudal fin by a notch. The dorsal finlets are the only fins with spines.

Polypteriforms have a compact, dense covering of trapezoidal, shiny (ganoid) scales, arranged in numerous diagonal series, which give them a rigid texture (similar to gars). Scales along the lateral line vary from about 55 to 70. Internally, polypteriforms have paired, asymmetrical (right lobe larger than left), and highly vascularized swim bladders that function as air-breathing organs. Coloration is olive-brown to dark brown dorsally and laterally, and over the head, but creamy white ventrally. Numerous dark or clear spots and blotches and irregular stripes are present in many species, sometimes over pectoral fins (e.g., *P. ornatipinnis*), but others are more uniform in color (*P. senegalus*). The heads of most species have a mottled or reticulated appearance.

Distribution

Present in western and central tropical Africa, with three species also occurring in the Nile River. They are absent from rivers that drain into the Indian Ocean.

Habitat

Commonly found in both fast and slow moving rivers, floodplains, swamps, lakes, and pools. Because they are able to breathe air directly, bichirs and the reedfish are capable of living in stagnant waters. They enter rivers with associated marginal vegetation during the spawning season.

Behavior

Not many studies documenting polypteriform behavior have been conducted. They are reported to "walk" over land for small distances to feed on insects, as they are able to absorb oxygen directly from the air for at least a few hours. However, air breathing is not obligatory, as it is in lepidosirenid lungfishes. In aquaria their behavior varies from remaining motionless on the bottom for short periods to swimming about vigorously. Their pectoral fins function as paddles.

Feeding ecology and diet

Polypteriforms are carnivorous, feeding on invertebrates such as insect larvae, snails, earthworms, and freshwater crustaceans, as well as fishes and amphibians; they are primarily nocturnal predators. Polypteriforms are preyed upon by crocodiles and large, fish-eating birds.

Reproductive biology

Reproduction has been observed in aquaria for a few bichir species as well as for the reedfish. Males may compete for the attention of a female. The anal fins are sexually dimorphic, as males have a pronounced bulge at the anal fin origin (anal fin is broader and more muscular). This modification develops gradually with sexual maturity; otherwise the fin is identical in both sexes. The anal fin is important during spawning, as the male will use his anal and caudal fins to envelop the genital opening of the female, thereby forming a receptacle in which he will fertilize her eggs. Eggs are then released by the male, through vigorous shaking of the anal fin, and quickly adhere to vegetation. This behavior has been described for both polypteriform genera. The larvae have feathery external gills. Polypterids do not practice any form of parental care of their eggs or fry.

Conservation status

No species are presently threatened or protected under CITES legislation, and none are listed in the IUCN database.

Significance to humans

Imported with frequency in the ornamental fish trade. The larger bichirs are highly regarded food fishes in West Africa. Their firm, white flesh tastes very much like the freshwater prawns that constitute an important part of the human diet in this region. These are very long-lived fishes, with records of large bichirs living 50 years in captivity.

Species accounts

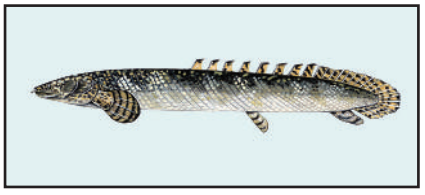
Bichir
Polypterus ornatipinnis

FAMILY
Polypteridae

TAXONOMY
Polypterus ornatipinnis Boulenger, 1902, Congo River.

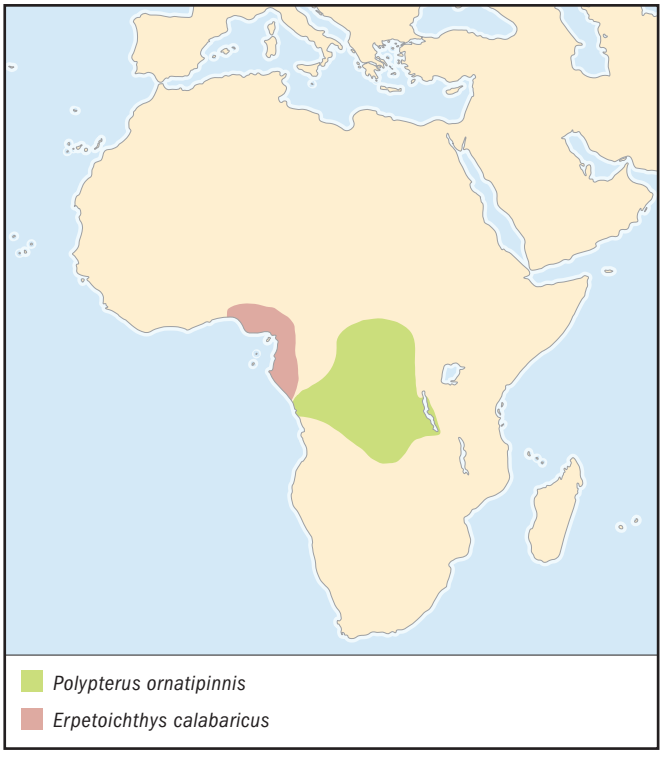
OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum length 23.6 in (60 cm). Body protected by an armor of large, rhombic, bony scales. Moderately elongate, with nine to 10 independent dorsal finlets. Pelvic fins located posteriorly. White belly with dark mottling on head, flanks and dorsum, with continuous parallel bands on fins.



Polypterus ornatipinnis

DISTRIBUTION
Central and East Africa, found in the Congo Basin and in Lake Tanganyika.



HABITAT
Lakes, rivers, floodplains, and swamps, including waters with low oxygen content.

BEHAVIOR
Often sits motionless on the bottom, resting on its pectoral fins such that the head and anterior portion of the body are slightly elevated. Periodically gulps air from the surface in stagnant water.

FEEDING ECOLOGY AND DIET
Carnivorous; feed mostly at night on a variety of prey, including other fishes, frogs, insects, and crustaceans.

REPRODUCTIVE BIOLOGY
During courtship, their usual inactivity is abandoned, and both male and female engage in energetic twisting, turning, and darting movements. The male subsequently envelops the female's genital opening with his anal and caudal fin, fertilizing the eggs and then scattering them by thrashing his tail.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Found in markets as a food fish; also captured for the aquarium trade. ◆

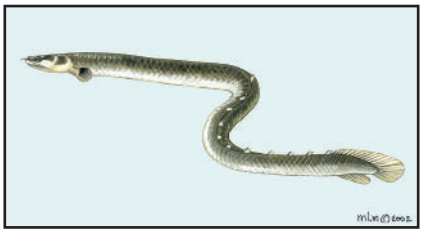
Reedfish
Erpetoichthys calabaricus

FAMILY
Polypteridae

TAXONOMY
Erpetoichthys calabaricus Smith, 1866, Old Calabar, West Africa.

OTHER COMMON NAMES
English: Ropefish.

PHYSICAL CHARACTERISTICS
Maximum length 35.4 in (90 cm). Shares with *Polypterus* rhombic bony scales and distinct dorsal finlets. Unlike *Polypterus*, *Erpetoichthys* lacks pelvic fins and is very elongate and eel-like in appearance. Uniform brown-olive color dorsally, with white underside and black spot on pectoral fins. Sexually active individuals develop an orange-red flush on the venter.



Erpetoichthys calabaricus

DISTRIBUTION
Coastal drainages of West Africa, from Nigeria to the Republic of the Congo.

HABITAT
Areas with aquatic vegetation in swamps and along rivers.

BEHAVIOR
Hunts along the bottom, moving in serpentine fashion.

FEEDING ECOLOGY AND DIET
Nocturnal predator, feeds on worms, crustaceans, and insects.

REPRODUCTIVE BIOLOGY
Very similar to that of *Polypterus*, in which the males wraps his anal fin around the female's genital pore, fertilizes the eggs, and then scatters them into the surrounding vegetation with vigorous tail thrashing. In Benin and Nigeria, ripe individuals undertake mass movements overland into seasonally flooded swamp pools in order to spawn.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
A popular aquarium fish.

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Marcelo Carvalho, PhD
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Acipenseriformes
(Sturgeons and paddlefishes)

Class Actinopterygii
Order Acipenseriformes
Number of families 2

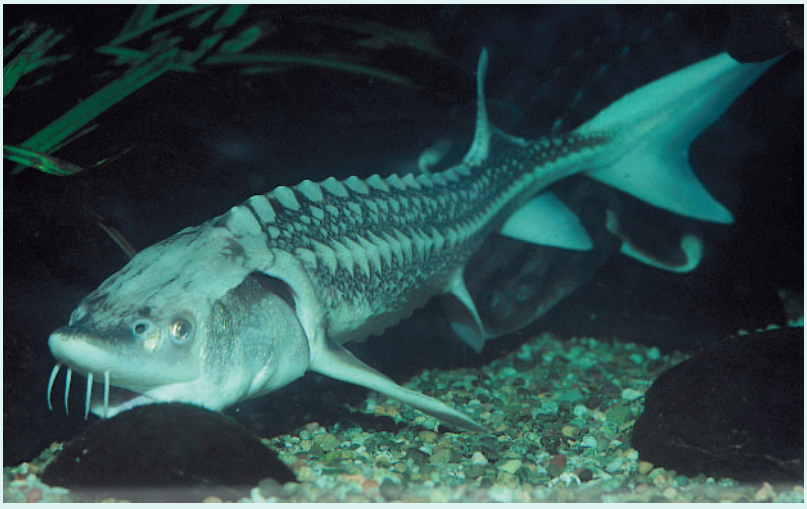


Photo: Sturgeons (*Acipenser gueldenstaedtii* is shown here) produce cavier prized globally, and this has resulted in a decline of sturgeon populations. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Acipenseriformes includes 25 species of sturgeons in four genera (*Acipenser*, *Huso*, *Scaphirhynchus*, and *Pseudoscaphirhynchus*) in the family Acipenseridae and two living species of paddlefishes in the family Polyodontidae. The Acipenseriformes are primitive fish; recognizable fossils date to the early Cretaceous (144–65 million years ago). The Acipenseridae and Polyodontidae probably diverged from each other during the Jurassic (208–146 million years ago).

Physical characteristics

Acipenseriformes are some of the largest freshwater fishes, with species ranging in maximum size from 2.5 ft (0.76 m) to nearly 28.2 ft (8.6 m). Their bodies are elongate with large heads, small eyes, and fins positioned towards the posterior. A lateral line and scales are absent. Sturgeons and paddlefishes are dark on the tops of their bodies, but pigmentation fades to much lighter ventral colors, and many have white bellies. Species of sturgeon take on a variety of dull colors: gray, brown, dark blue, olive-green, and nearly black. Paddlefishes may appear bluish gray, brown, or black on their dorsal surface.

All Acipenseriformes share relict characteristics, including a largely cartilaginous endoskeleton and heterocercal caudal fin. The only ossified bones are found in the skull, jaws, and pectoral girdle. Other common anatomical features include an elongated snout with sensory barbels, a ventral mouth, an unconstricted notochord, and a lack of scales covering their skin.

Although they share many similar characteristics, anatomical and ecological distinctions exist between sturgeons and paddlefishes. Sturgeons have four barbels used for detecting prey, and the ventral mouth is protrusible. Paddlefishes have only two small sensory barbels and nonprotrusible mouths. Another major anatomical difference between sturgeons and paddlefishes is in their body coverings. The skin of paddlefishes is largely naked, with patches of minute scales. In contrast, sturgeons are armored with five rows of bony shields along their bodies.

Distribution

Acipenseriformes are found throughout the Northern Hemisphere in North America, Europe, and Asia. Among the sturgeons, nine species inhabit North America, four are found in Europe, ten live in Asia, and four have Eurasian distributions. One species of paddlefish is found in North America; the other paddlefish species is endemic to China.

Habitat

Acipenseriformes inhabit seas, rivers, and lakes. Some species spend a large portion of their lives at sea but enter coastal rivers to spawn. Other species live strictly in freshwater rivers and lakes. Sturgeons are typically associated with sand, gravel, or rock substrates.

Behavior

Most sturgeons spend their lives in their native river or in nearshore areas of adjacent seas, but some individuals move long distances through coastal habitats. Sturgeons exhibit seasonal and spawning migrations. They may move from shallow to deep water in the summer and return to shallow areas in the winter. All sturgeons spawn in fresh water; thus, those that live in the sea migrate to fresh water for spawning. Paddlefishes swim constantly, both day and night, and migrate upstream to spawn.

Sturgeons are active primarily during the day, and many species congregate in discrete seasonal feeding areas.

Fish farm workers catch a 15-year-old Chinese sturgeon in order to inject it with hormones and make it produce eggs that will later be artificially fertilized, at Yichang, in China's Hubei province. The fish, which can grow up to 13 ft (4 m) long and weigh more than 1,000 lb (454 kg), are threatened by hydropower projects. The dams have affected the sturgeon's spawning grounds in the Yangtze, prompting authorities in 1982 to set up the "Chinese Sturgeon Park" in Yichang to breed the fish artificially. (Photograph. AP/Wide World Photos. Reproduced by permission.)

Observations of lab-reared juveniles suggest that certain species may establish a dominance hierarchy based on size, with large fish acting aggressively towards smaller fish in disputes over limited foraging space. Although sturgeons and paddlefishes are solitary for most of their life, some aggregation has been observed in larvae, which migrate in unorganized groups.

Feeding ecology and diet

Sturgeons locate food by swimming close to the bottom with their sensory barbels dragging the substrate. They selectively ingest slow-moving benthic invertebrates, including insects, worms, crustaceans, and mollusks, and feed on other fishes to a limited extent. Paddlefishes feed by swimming through the water with their mouths open and filtering large amounts of water through their gill rakers. Paddlefishes primarily consume microcrustaceans and insect larvae in the plankton, but they occasionally eat benthic invertebrates and other fishes.

Because of their large size and protective bony scutes, adult sturgeons and paddlefish have few predators except humans. However, sturgeons may be attacked, and possibly killed, by the parasitic sea lamprey, *Petromyzon marinus*.

Reproductive biology

Sturgeons typically spawn during spring and summer months. Prespawning activities involve rolling near the bottom and leaping out of the water. Spawning takes place in groups of two to three fish, with one or two males per female. Female sturgeons produce large quantities of eggs (up to several million), which are deposited over shallow shoals or rocky areas and fertilized by males. No nests are constructed, but the eggs are adhesive and stick to the substrate. Sturgeons do not devote any parental care to their offspring. Adults of some species spawn every year, but most species allow longer intervals between spawning events.

Paddlefishes spawn in the early spring as water levels are rising. They migrate from lakes and rivers into streams to locate spawning sites in shallow water. Males and females broadcast eggs and sperm over gravel substrates while swimming in groups. No parental care is provided to the offspring. Female paddlefishes produce very large numbers of eggs (up to 600,000) and do not spawn annually.

Conservation status

Overexploitation and habitat alteration, particularly the construction of dams, threaten and limit populations of Acipenseriformes throughout their range. The commercial landings of sturgeons exceeded 3,000 tons (2,721 tonnes) in 1890, but landings declined by 99% over the next century. Overfishing threatened many populations with local extinction, and stock enhancement programs have been introduced to maintain many sturgeon fisheries. Dams limit access to spawning sites and isolate populations. Other human activities on the shores of rivers increase siltation and contaminate rock or gravel spawning areas.

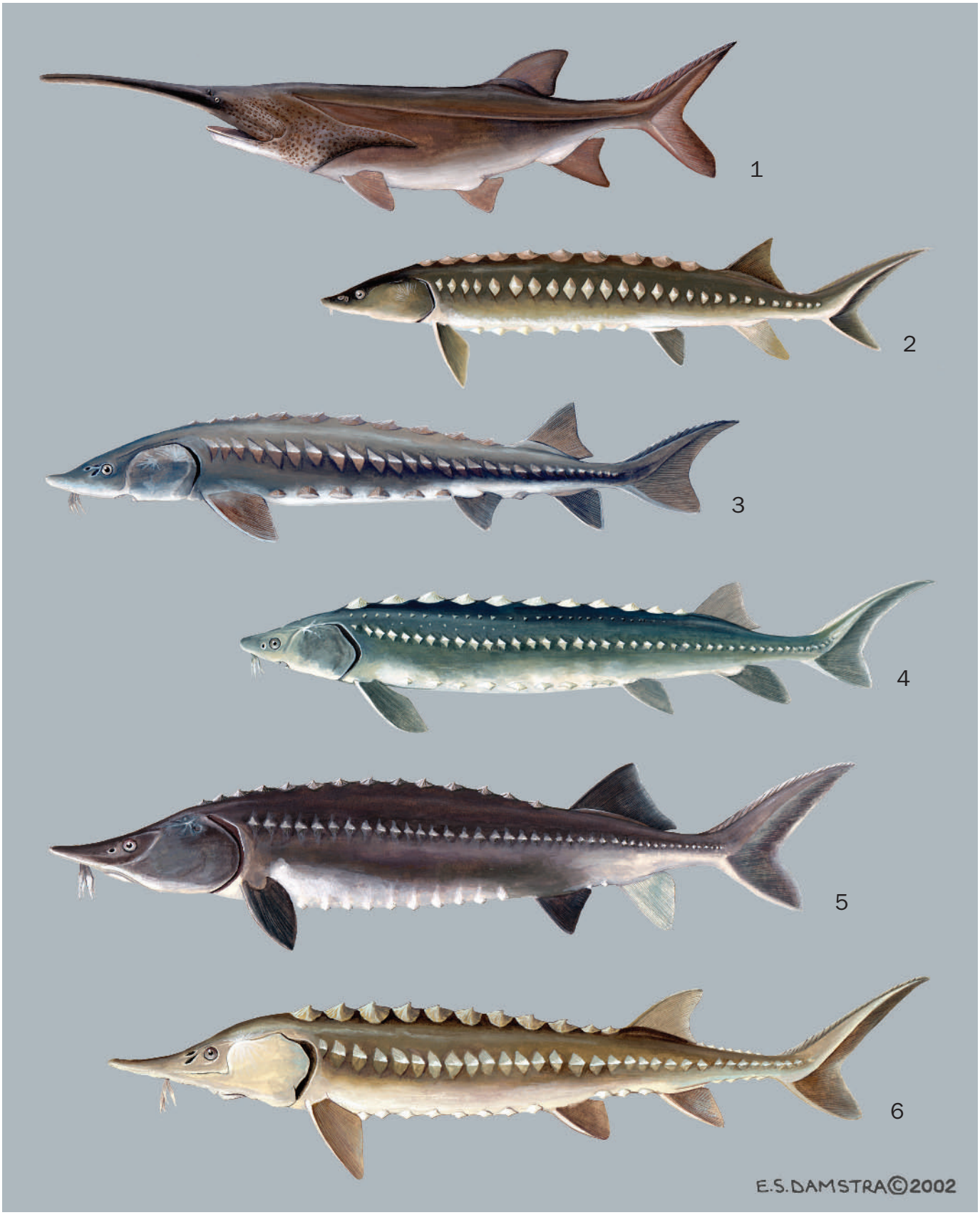
A lake sturgeon (*Acipenser fulvescens*) hovering over the sandy bottom. (Photo by Tom McHugh/Steinhart Aquarium/The National Audubon Society/Photo Researchers, Inc. Reproduced by permission.)

All Acipenseriformes are cited on the IUCN Red List. While some species are considered Lower Risk/Near Threatened (2 species) by the IUCN, most species are at greater risk and are classified as either Critically Endangered (6 species), Endangered (11 species), or Vulnerable (8 species). The international trade of Acipenseriformes is regulated through the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). The shortnose sturgeon (*Acipenser brevirostrum*) and the common sturgeon (*Acipenser sturio*) are considered threatened with extinction and are listed on Appendix I of CITES. All other species of sturgeon and paddlefish are listed on Appendix II of CITES. The shortnose sturgeon is listed as an endangered species in the United States.

Paddlefishes (*Polydon spathula*) do not have teeth, and eat by swimming through the water with their mouths open, scooping up plankton. (Photo by Daniel Heuclin/BIOS. Reproduced by permission.)

Significance to humans

Sturgeons have been valued for their caviar, the unfertilized eggs of the female, since the times of the ancient Persian, Greek, and Roman empires. The Chinese began trading caviar during the tenth century. It became popular as a luxury food in Europe during the seventeenth and eighteenth centuries and remained prized as a culinary delicacy at the end of the twentieth century. The smoked meat of sturgeons also is highly valued, particularly in European and Asian markets. In the late 1800s, paddlefish eggs and flesh also were sought commercially.



1. American paddlefish (*Polyodon spathula*); 2. Shortnose sturgeon (*Acipenser brevirostrum*); 3. Lake sturgeon (*Acipenser fulvescens*); 4. White sturgeon (*Acipenser transmontanus*); 5. Beluga sturgeon (*Huso huso*); 6. Atlantic sturgeon (*Acipenser oxyrhinchus*). (Illustration by Emily Damstra)

Species accounts

Shortnose sturgeon
Acipenser brevirostrum

FAMILY
Acipenseridae

TAXONOMY
Acipenser brevirostrum LeSueur, 1818, Delaware River, United States.

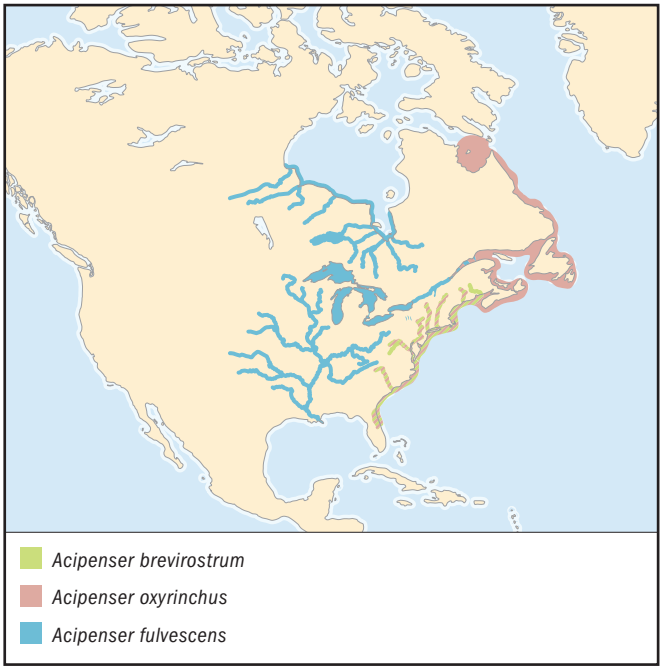
OTHER COMMON NAMES
English: Shortnosed sturgeon; French: Esturgeon à nez court; Spanish: Esturión hociquicorto.

PHYSICAL CHARACTERISTICS
At approximately 3 ft (0.9 m) in length, the shortnose sturgeon is the smallest species in the genus *Acipenser*. It has a shorter snout than other sturgeons and a wide mouth. Its upper body is dark brown or black, with lighter colors on the ventral portion. The bony plates are light in color.

DISTRIBUTION
Shortnose sturgeons occur along the East Coast of North America, from St. John River in New Brunswick, Canada, to Indian River, Florida.

HABITAT
Shortnose sturgeons live in the ocean, estuaries, and large coastal rivers.

BEHAVIOR
Shortnose sturgeons migrate upstream and downstream seasonally in coastal rivers. In southern portions of the range, these fishes spend longer periods of time at sea and migrate into rivers to spawn. Juvenile shortnose sturgeons may compete for limited foraging space, and larger individuals become aggressive to ward off encroaching individuals of smaller size.



FEEDING ECOLOGY AND DIET
Shortnose sturgeons are opportunistic benthic feeders. Young individuals eat insects and crustaceans. Adults consume mollusks, benthic crustaceans, polychaete worms, and insect larvae.

REPRODUCTIVE BIOLOGY
Male shortnose sturgeons first spawn around three to four years of age, and females first spawn between six and fifteen years. Spawning takes place in the spring over gravel or rocky substrates. Females can produce 200,000 eggs per fish, and eggs hatch after approximately 13 days. Females spawn at intervals of three to five years, but males may spawn every year.

CONSERVATION STATUS
The shortnose sturgeon is listed as Vulnerable by the IUCN and protected under Appendix I of CITES. It also is recognized as an endangered species under the U.S. Endangered Species Act and as a vulnerable species by the Committee on the Status of Endangered Wildlife in Canada.

SIGNIFICANCE TO HUMANS
The caviar and flesh of shortnose sturgeons were commercially important during the 1800s and 1900s. Populations began declining in the 1800s due to industrial pollution of rivers and overfishing. As of 2002, all fisheries for this species are closed. ◆

Lake sturgeon
Acipenser fulvescens

FAMILY
Acipenseridae

TAXONOMY
Acipenser fulvescens Rafinesque, 1917, Lake Erie, North America.

OTHER COMMON NAMES
English: Freshwater sturgeon, Great Lakes sturgeon; French: Esturgeon jaune; Spanish: Esturión lacustre.

PHYSICAL CHARACTERISTICS
The back and sides of large lake sturgeon are olive-brown to dull gray in color; juveniles are light brown with dark blotches. Most lake sturgeons today are 3–5 ft (0.9–1.5 m) long and weigh 10–80 lb (4.5–36.3 kg), but a female of nearly 8 ft (2.4 m) and 310 lb (140.6 kg) has been documented.

DISTRIBUTION
Lake sturgeons occur in the following North American drainages: Great Lakes, St. Lawrence River, Hudson Bay, and Mississippi River.

HABITAT
Lake sturgeons inhabit large rivers and lakes.

BEHAVIOR
Lake sturgeons migrate seasonally between shallow and deeper waters, particularly in the northern extent of their range. They also undertake extensive migrations, typically of around 80 mi (128.7 km), to find suitable spawning grounds in rivers.

FEEDING ECOLOGY AND DIET
Lake sturgeons primarily consume insects, as well as other benthic invertebrates, such as snails, clams, and crayfishes. They occasionally feed on fish eggs, algae, and small fishes.

REPRODUCTIVE BIOLOGY
Lake sturgeons first spawn at 14–23 years for females and 12–20 years for males. Spawning intervals range from two to seven years in males and four to nine years in females. In the spring when ice clears, lake sturgeons migrate into smaller rivers and streams for spawning. Spawning typically takes place in swift-moving water 2–15 ft (0.6–4.6 m) deep. In the Great Lakes, lake sturgeons spawn along rocky shores in groups of two to three individuals. Females shed eggs in batches over a period of days. The eggs adhere to rocks for five to eight days before hatching.

CONSERVATION STATUS
Populations of lake sturgeons are threatened because of human exploitation, as well as habitat alteration and fragmentation that is caused by the construction of dams and roads. Lake sturgeons are listed as Vulnerable by the IUCN. They are protected by state and provincial fishing regulations and habitat restoration efforts in the United States and Canada.

SIGNIFICANCE TO HUMANS
Lake sturgeons were harvested for food by Native Americans before Europeans settled in North America, and commercial markets developed for the eggs and smoked flesh in the mid-1800s. Isinglass, a gelatin obtained from the swim bladder, was used to make jam and jellies, as a pottery cement, and as a waterproofing agent. Recreational fishing for lake sturgeons remains popular. ◆

Atlantic sturgeon
Acipenser oxyrinchus

FAMILY
Acipenseridae

TAXONOMY
Acipenser oxyrinchus oxyrinchus Mitchill, 1815, New York, United States. Two subspecies are recognized.

OTHER COMMON NAMES
English: Sea sturgeon, common sturgeon.

PHYSICAL CHARACTERISTICS
The Atlantic sturgeon is a large species that often grows to over 10 ft (3 m) long. Individuals are blue-black in color, with lighter shades on the sides. The head, ventral portion of the body, and fin edges are typically white.

DISTRIBUTION
Atlantic sturgeons are found along the Atlantic coast of North America from Ungava Bay, Quebec, to the St. John's River in Florida.

HABITAT
This species lives in the ocean and in bays, estuaries, and rivers.

BEHAVIOR
Atlantic sturgeons migrate between the sea and freshwater. Juveniles spend several years in freshwater before first entering the sea. Most individuals remain near their native river, but some travel long distances over the continental shelf. The migratory behavior of this species is typically associated with spawning activities, but some individuals move into freshwater and do not spawn. Some evidence suggests that Atlantic sturgeons establish priority for foraging areas based on body size, with larger individuals dominant over smaller ones for feeding space.

FEEDING ECOLOGY AND DIET
Atlantic sturgeons consume bottom-dwelling plants and animals, such as insects, crustaceans, and mollusks. As adults, they also eat small fish.

REPRODUCTIVE BIOLOGY
Male Atlantic sturgeons typically reach sexual maturity around 12–24 years of age, and females are capable of spawning at 18–28 years. It is believed that females spawn in approximately four-year intervals, whereas males may spawn every year. The spawning season extends from late spring to early summer. Eggs are demersal and adhere to substrates near the spawning area.

CONSERVATION STATUS
Although populations have declined due to habitat alteration and fishing activities, Atlantic sturgeons are not considered threatened or endangered in the United States or Canada. They are listed as Lower Risk/Near Threatened by the IUCN.

SIGNIFICANCE TO HUMANS
Atlantic sturgeons are valuable for their flesh and roe, with colonial fisheries extending back to the 1600s. In the United States, commercial fisheries for Atlantic sturgeons were closed in 1998, although fishing had ceased in many states before that date. Commercial fishing continues in the St. Lawrence and St. John Rivers of Canada. ◆

White sturgeon
Acipenser transmontanus

FAMILY
Acipenseridae

TAXONOMY
Acipenser transmontanus Richardson, 1836, Vancouver, Washington, United States.

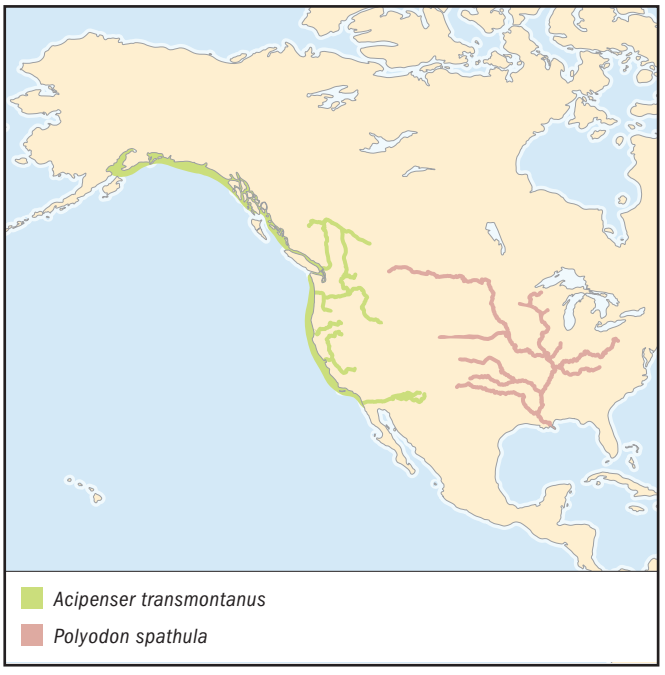
OTHER COMMON NAMES
English: Pacific sturgeon, Columbia sturgeon, Oregon sturgeon; French: Esturgeon blanc.

PHYSICAL CHARACTERISTICS
The white sturgeon is the largest North American sturgeon, attaining a maximum length of 20 ft (6.1 m). The upper body is gray, olive, or gray-brown, and its lower body is light gray to white.

DISTRIBUTION
Native distribution of the white sturgeon is along the Pacific coast of North America from the Aleutian Islands, Alaska, to Monterey, California. Landlocked populations occur in Montana and California. The species has also been introduced in the Colorado River in Arizona.

HABITAT
White sturgeons populate the ocean, estuaries, rivers, and lakes.

BEHAVIOR
White sturgeons spend most of their lives at sea but enter large rivers to spawn. Some individuals move long distances in coastal migrations.



FEEDING ECOLOGY AND DIET
Juvenile white sturgeons feed on benthic invertebrates, such as chironomids, mollusks, and crustaceans. Adults primarily consume other fishes, shellfish, and aquatic invertebrates.

REPRODUCTIVE BIOLOGY
White sturgeons usually spawn in May or June in swift waters over rocky substrates. Males spawn initially between 11 and 22 years of age; females do not spawn until they are between 26 and 34 years. Younger females spawn every four years, while the interval increases to nine to eleven years for older females. The largest female spawners may produce three to four million eggs.

CONSERVATION STATUS
White sturgeons are classified as Lower Risk/Near Threatened by the IUCN. This species has been particularly affected by the damming of rivers. Populations were also severely overfished, but successful stocking programs and fishing regulations have enabled recovery.

SIGNIFICANCE TO HUMANS
White sturgeons have been used by Native Americans in the northwest region of the United States since long before the arrival and settlement of Europeans in the area. A commercial fishery for white sturgeons began on the Columbia River in the late 1800s, but the stock was depleted within a decade. Strict regulations put in place during the 1950s led to a population recovery by the late 1990s. By the early twenty-first century, commercial, recreational, and tribal fisheries actively targeted white sturgeons throughout their range. ◆

Beluga sturgeon
Huso huso

FAMILY
Acipenseridae

TAXONOMY
Huso huso Linnaeus, 1758, Danube and rivers of Russia.

OTHER COMMON NAMES
English: European sturgeon, great sturgeon.

PHYSICAL CHARACTERISTICS
The beluga sturgeon is the largest sturgeon species. It has been recorded to attain a length of 28.2 ft (8.6 m) and weight of 2,866 lb (1,300 kg), although such large specimens are rare. The body is gray or dark green in color with lighter sides and a white belly.

DISTRIBUTION
Beluga sturgeons occur in the Black, Caspian, and Adriatic Seas and in most of their tributaries.

HABITAT
This species inhabits nearshore areas of seas and large channels of rivers.

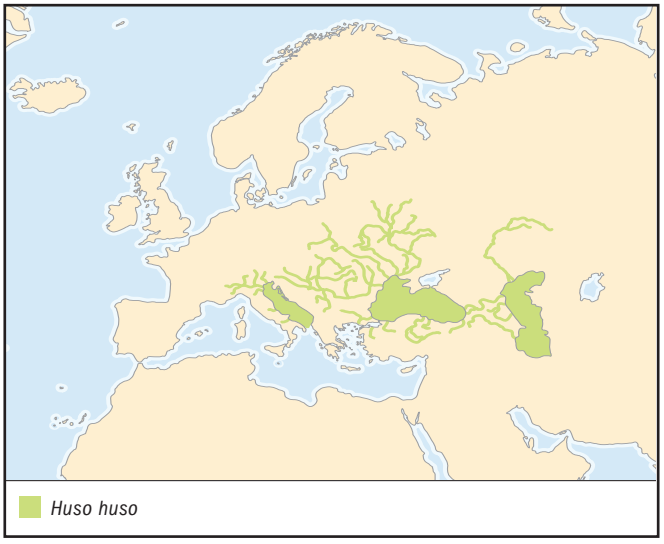
BEHAVIOR
Adult beluga sturgeons live at sea for most of the year but migrate up large river tributaries for spawning. The fry, or young fish, move downstream from rivers to the sea immediately after hatching.

FEEDING ECOLOGY AND DIET
Juvenile beluga sturgeons feed on benthic invertebrates, such as mollusks, worms, and crustaceans; adults eat other fishes.

REPRODUCTIVE BIOLOGY
Beluga sturgeons mature slowly and are extremely long lived (up to 150 years). Sexual maturity occurs around 14 years of age for males and 18 years for females. Females may produce over seven million eggs, but reproduction only occurs once every five to seven years. Beluga sturgeons spawn in late spring by scattering eggs and sperm in the water over rocky substrates.

CONSERVATION STATUS
The beluga sturgeon is listed as Endangered on the IUCN Red List. It may be extinct in the Adriatic Sea, and populations have declined throughout its range. The Caspian population is made up largely of fish from stocking programs.

SIGNIFICANCE TO HUMANS
Beluga sturgeons are valued throughout the world as the source of superior caviar. The caviar commands high prices, and the market demand has driven fisheries in eastern Europe to continue exploitation despite severe population declines. ◆



American paddlefish

Polyodon spathula

FAMILY
Polyodontidae

TAXONOMY
Polyodon spathula Walbaum, 1792, Louisiana, Mississippi River, United States.

OTHER COMMON NAMES
English: North American paddlefish, Mississippi paddlefish, spoonbill cat; French: Poisson spatule.

PHYSICAL CHARACTERISTICS
A defining characteristic of the American paddlefish is its large paddle-shaped rostrum, or snout. The paddle is covered with electroreceptors that enable paddlefish to sense objects and concentrations of planktonic prey. American paddlefish live up to 30 years and may attain lengths of 6.6 ft (2 m) and weights of 190 lb (86.2 kg).

DISTRIBUTION
American paddlefishes currently occur within the Mississippi River and Mobile Basin drainages in the United States, although the historical distribution included the Laurentian Great Lakes of Canada.

HABITAT
This species is found in large rivers and lakes.

BEHAVIOR
American paddlefishes swim continuously, often moving long distances. They typically are found near the water surface and frequently leap from the water.

FEEDING ECOLOGY AND DIET
American paddlefishes swim through the water with their mouths open and feed passively by filtering zooplankton and larvae of aquatic insects. Other fishes are occasionally found in stomach samples, indicating that paddlefishes are not strictly filter feeders.

REPRODUCTIVE BIOLOGY
Male paddlefishes mature between seven and nine years of age; females, between 10 and 12 years. Females may produce up to 600,000 eggs. Paddlefishes spawn in fast-flowing waters with clean gravel bottoms at intervals of two to five years. Spawning takes place in early spring in water depths of approximately 10 ft (3 m). Eggs and sperm are broadcast into the water column; eggs stick to the substrate and hatch within about seven days.

CONSERVATION STATUS
American paddlefishes are listed as Vulnerable by the IUCN. This species once occurred throughout the Mississippi River system, but habitats were fragmented by damming of the main stem of the Mississippi and its tributaries. Paddlefishes have been overfished, but state regulations and stocking programs are attempting to restore populations. Although fishing for paddlefishes is prohibited in most states, a few states allow commercial and recreational fisheries that target this species.

SIGNIFICANCE TO HUMANS
Like sturgeons, paddlefishes are valued for their flesh and roe. An important commercial fishery existed for paddlefishes in the Mississippi Valley following the decline of the sturgeon fishery in 1895, but this fishery reached its peak in 1900.

Resources

Books

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Katherine E. Mills, MS

Lepisosteiformes
(Gars)

Class Actinopterygii
Order Lepisosteiformes
Number of families 1

Photo: The spotted gar (*Lepisosteus oculatus*) is frequently found in the pet trade. (Photo by Garold W. Sneegas. Reproduced by permission.)

Evolution and systematics

Lepisosteiformes contains the extant family Lepisosteidae (the gars). Extinct families that may belong in the order include the Semionotidae. The order Lepisosteiformes is sometimes classified within the division Ginglymodi.

The family Lepisosteidae includes seven living species contained in two genera, *Lepisosteus* and *Atractosteus*. Fossil gars are known as far back as the early Cretaceous period. The earliest fossil gars are represented only by scale, teeth, or bone fragments, but there are complete skeletons known as far back as 110 million years.

The gars have sometimes been included within the order Semionotiformes because of a presumed close relationship with the Semionotidae. More recently, this relationship has come into question. Consequently, the ordinal name Lepisosteiformes as used in this chapter contains the gars, and the Semionotiformes includes Semionotidae, but excludes the gars.

The gars comprise one of only five living actinopterygian families not contained within Teleostei (a group containing over 25,000 living species). They have often been referred to as "living fossils," and understanding their morphology is important to deciphering the evolutionary relationships of ray-finned fishes. Some authors have placed the gars within Holostei (together with bowfins), but they are thought by most systematic ichthyologists to comprise the living sister group to Halecostomi (a group containing bowfins and teleosts, but excluding gars). Whether to recognize Holostei (grouping gars with bowfins) or Halecostomi (placing gars outside of a bowfin/teleost group) remains controversial. Morphological data supports Halecostomi, whereas molecular data supports Holostei. It has even been suggested that gars and teleosts form a monophyletic group that excludes bowfins, although this phylogenetic hypothesis has not been widely accepted.

Physical characteristics

Extant lepisosteids and many of the fossils have a similar appearance. They have a highly elongate snout or "bill," well-armored elongate bodies covered with interlocking rhomboid-shaped ganoid scales, posteriorly positioned median fins with a dorsal fin set above the anal fin, a "tongue" supported by a number of bony basihyal tooth plates, and a jaw articulation anterior to the orbit. They also have an "abbreviate heterocercal" caudal fin, in which the hypurals (caudal ray supports) attach proximally with the ventral surface of the upturned end of the vertebral column. Gars also have a number of extremely diagnostic small features that enable the identification of even fragmentary fossils as gars. These features include plicidentine teeth (a peculiar folded dentine structure surrounding the pulp cavity) and opisthocoelous vertebrae (vertebral centra that are convex anteriorly and concave posteriorly). The ganoid scales are also diagnostic among living fishes, although the scales of African polypterids are superficially similar.

Distribution

Extant gars are restricted to freshwaters of eastern North America, as far north as Montana, United States, and southern Quebec, Canada, and as far west as Montana; Central America; and Cuba. When fossil (extinct) species are included, gars comprise a much greater diversity and geographic range. Well-preserved fossil gar material extends the geographic range of the family into what are now parts of western North America, Europe, Africa, Madagascar, India, and South America. Fossil and living gars are notably absent from East Asia. The one report of a living gar from China (*Lepisosteus sinensis* Bleeker, 1873) was in error, and was a belonid (Teleostei) rather than a lepisosteid.

Habitat

Gars are primarily freshwater fishes, although some species are known to occasionally swim into brackish or nearshore marine environments. The alligator gar, *Atractosteus spatula*, in particular, is frequently caught by shrimp trawlers in the salt marshes of Louisiana, and has often been observed in waters of the Gulf Coast.

Gars can withstand aquatic environments of low oxygen content because their swim bladder is highly vascularized and

Longnose gars (*Lepisosteus osseus*) can breathe through their air bladders and thus can tolerate poorer water conditions. (Photo by Garold W. Sneegas. Reproduced by permission.)

connected to the pharynx by an enlarged pneumatic duct, allowing them to breathe air.

Behavior

Gars are generally sluggish, but are capable of extremely quick movements for short periods of time. They often lie motionless near the surface until prey swims within reach. Then with a quick sideways thrust of its sharply toothed bill, the fish impales the food item and eventually swallows it. Although alligator gar reach a very large size (up to 9.8 ft/3 m total length) and have numerous, large, sharply pointed teeth and a head that superficially resembles that of a crocodilian, there are no authenticated records of any serious attacks on humans.

Feeding ecology and diet

Gars are primarily piscivorous, although most species supplement their diet with frogs, invertebrates, or even refuse that is dumped into the water. Gars are occasionally cannibalistic. The elongate, well-toothed jaws of gars facilitate the grasping of swimming prey with quick movements of the head. Large alligator gars also occasionally feed on water birds. Adult gars are well armored with their thick scales and dermal bones; consequently, they have few predators.

Reproductive biology

Gars spawn in freshwater generally in the spring (e.g., mid-May to mid-June in New York, United States). Fertilization is external, and large numbers of individuals concentrate in shoal areas and disperse quickly afterward. No parental care is given to the eggs or young. The eggs are black in color, adhesive, and stick to the substrate, rocks, or plants. After hatching, the larvae have adhesive suckers that enable them to stick to objects, even in moving water. The eggs are highly toxic.

Conservation status

No species of gars are included on the IUCN Red List. Most species are quite abundant, although the alligator gar is becoming very rare in some areas of its former range. Sport fishing for alligator gars is popular in some areas of the southeastern United States. Because the species are widely perceived by sport fishermen as being detrimental to game fishes, these fishes have received little sympathy. There have been efforts to manage alligator gars, and they have been declared an endangered species in some of the southeastern states.

Significance to humans

Gars are often thought of as a nuisance fish detrimental to game fishes, and they often break up the nets of commercial fishermen in the southeastern states; but alligator gars are important predators in most aquatic ecosystems where they occur. The flesh of gars is extremely bony and not generally used for food. Exceptions include New Orleans and some other regions of the southeastern United States where alligator gar meat is sold, and the Pacific side of southern Mexico and Guatemala where the tropical gar is an important food item. The eggs of gars are toxic.

The ganoid scales of gars have historically been used for jewelry, arrowheads, and ornaments.

Alligator gars are popular sport fishes in the southern United States, and have inspired "fishing rodeos" and other tournaments. The Florida gar, *Lepisosteus platyrhincus*, has an attractive color pattern which makes it a popular aquarium fish. The longnose, *Lepisosteus osseus*, spotted, *Lepisosteus oculatus*, and alligator gars occasionally turn up in the pet trade as well.

Alligator gars (*Atractosteus spatula*) in Everglades waters, Everglades National Park, Florida. (Photo by Jim Zipp/Photo Researchers, Inc. Reproduced by permission.)

1. Cuban gar (*Atractosteus tristoechus*); 2. Tropical gar (*Atractosteus tropicus*); 3. Longnose gar (*Lepisosteus osseus*); 4. Shortnose gar (*Lepisosteus platostomus*); 5. Spotted gar (*Lepisosteus oculatus*); 6. Florida gar (*Lepisosteus platyrhincus*); 7. Alligator gar (*Atractosteus spatula*). (Illustration by Emily Damstra)

Species accounts

Alligator gar
Atractosteus spatula

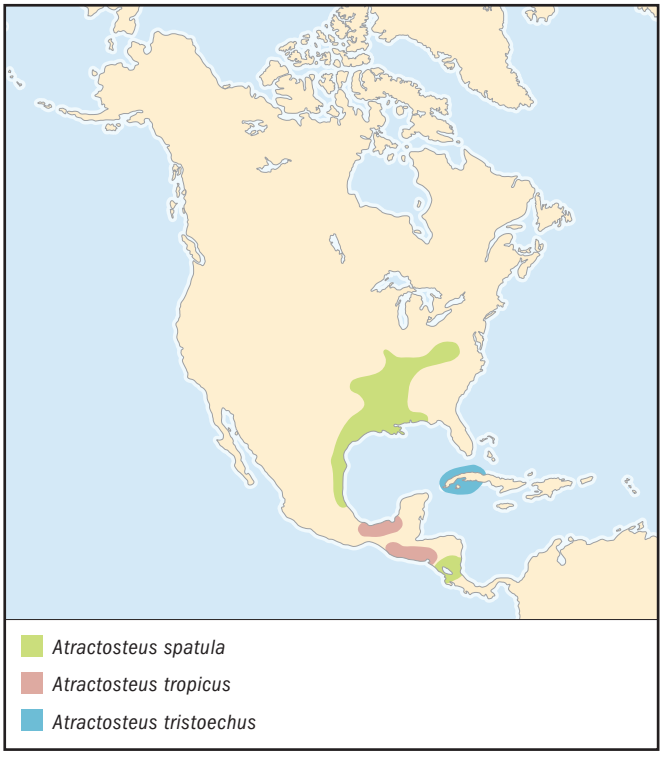
FAMILY
Lepisosteidae

TAXONOMY
Atractosteus spatula Lacépède, 1803 type locality not specified. "*Lepisosteus ferox*" Rafinesque, 1820. The type species for the genus *Atractosteus*, is a subjective junior synonym of *A. spatula*, making this species the effective species type of the genus *Atractosteus*.

OTHER COMMON NAMES
French: Garpique alligateur; Spanish: Catán, gaspar baba, pejelagarto.

PHYSICAL CHARACTERISTICS
Attains the largest size of any living gar, up to 9.8 ft (3 m) total length. One specimen has been reported at "9 feet 8.5 inches long and [weighing] 302 pounds" (2.8 m/137 kg). Adults usually have heavy ornamentation on exposed surfaces of the scales.

DISTRIBUTION
North America from Vera Cruz, Mexico, north through the Mississippi River drainage into southern Illinois, Indiana and Ohio, United States, and along much of the Gulf Coast. There is also a disjunct population reported from Lake Nicaragua and Rio Sapoá, Nicaragua. There are records of exotic introductions by humans as far west as California. Reported as a fossil from Pliocene deposits of Kansas and Pleistocene deposits of Texas and Florida, but fossils assigned to this species are isolated fragments (mostly scales) and somewhat tenuous in their assignment.



HABITAT
Freshwater river and swamp habitats, but also enters brackish and even marine waters. Of gar species, the most tolerant of salinity.

BEHAVIOR
Little is known besides feeding behavior.

FEEDING ECOLOGY AND DIET
Often portrayed as a voracious predator, although many reports are largely poorly documented sensationalism. As the largest, most solidly toothed gar, it is anatomically equipped to take a large variety of large prey, but this species is also a scavenger, and has been reported to compete with sharks for garbage at the wharves in Pensacola, Florida. The diet includes other fishes, blue crabs and other invertebrates, small mammals, and water birds such as ducks and water turkeys. Will prey opportunistically on alligator and crocodile hatchlings.

REPRODUCTIVE BIOLOGY
Very little is known about the reproductive habits. As in other gar species, the eggs are toxic to other animals.

CONSERVATION STATUS
Not threatened, although large individuals are taken in fish rodeos, spear fishing, and numerous annual contests.

SIGNIFICANCE TO HUMANS
Used for food and in sport fishing in the southern United States. Sometimes turns up in the pet trade. ◆

Cuban gar
Atractosteus tristoechus

FAMILY
Lepisosteidae

TAXONOMY
Atractosteus tristoechus Bloch and Schneider, 1801, Cuba. Sometimes confused with the alligator gar. It is distinguishable as a separate species, but in the late nineteenth and early twentieth centuries, several authors considered the Cuban gar (*A. tristoechus*) and the alligator (*A. spatula*) to be synonyms. Consequently, some authors referred to the alligator gar as "*A. tristoechus*" or "*L. tristoechus*," and museum specimens of alligator gars are sometimes labeled as "*tristoechus*." In the author's experience, museum specimens collected in North America labeled "*L. tristoechus*" or "*A. tristoechus*" are actually *A. spatula*.

OTHER COMMON NAMES
French: Garpique cubain; German: Alligatorhecht, Kaimanfisch; Spanish: Manjuari.

PHYSICAL CHARACTERISTICS
Not as large as the alligator gar; largest known specimen is 36.6 in (93 cm) total length. Caudal fin has a distinctive color pattern, with the fin outlined with a thin line of dark pigment.

DISTRIBUTION
Western Cuba and the nearby Isle of Pines.

HABITAT
Very little is known.

BEHAVIOR
Similar to that for entire order.

FEEDING ECOLOGY AND DIET
Based on stomach-content analysis, evidently feeds on other fishes, but further studies are still needed.

REPRODUCTIVE BIOLOGY
Very little is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Tropical gar
Atractosteus tropicus

FAMILY
Lepisosteidae

TAXONOMY
Atractosteus tropicus Gill, 1863.

OTHER COMMON NAMES
Spanish: Catán, gaspar, pejelagarto.

PHYSICAL CHARACTERISTICS
Small species; largest specimen known to the author is 49.2 in (125 cm) total length. Trunk is more pigmented than in other *Atractosteus* species.

DISTRIBUTION
Southern Mexico and Central America, with disjunct populations on both Atlantic and Pacific drainages

HABITAT
Freshwater rivers, streams, and near-shore lacustrine environments, but will occasionally enter brackish water.

BEHAVIOR
Visible on the surface and resemble floating logs.

FEEDING ECOLOGY AND DIET
Feeds mainly on fishes, but also may take copepods, insects, and plant material.

REPRODUCTIVE BIOLOGY
Reaches sexual maturity at about 14 in (36 cm) total length. Enters shallow lakes at beginning of dry season, spawning as rains cause flooding. Large schools form to lay eggs in a large gelatinous mass.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Spotted gar
Lepisosteus oculatus

FAMILY
Lepisosteidae

TAXONOMY
Lepisosteus oculatus Winchell, 1864, Duch Lake, Calhoun Co., Michigan, United States.

OTHER COMMON NAMES
French: Garpique tachetée; German: Gefleckter Knochenhecht; Spanish: Gaspar pintado.

PHYSICAL CHARACTERISTICS
Maximum total length (known to the author) is 32.9 in (83.5 cm), although reported up to 44 in (112 cm). Has a profusion of dark spots on the body, head, and fins (although these spots are not generally as large and strong as in the Florida gar). Adults have a series of small bony plates on the ventral surface of the isthmus. Females have been reported to have proportionately longer snouts than males.

DISTRIBUTION
Great Lakes south to the gulf coast of Texas, United States, and northern Mexico, east to northwestern Florida, United States. Reported as a fossil from Pleistocene deposits of Texas, but the material is too fragmentary to be reliably included in the species.

HABITAT
Quiet, clear waters with abundant vegetation, also brackish waters along the Gulf of Mexico.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Feeds mainly on fishes, but may also take crabs and crayfishes.

REPRODUCTIVE BIOLOGY
Spawns in shallow freshwater. Like *L. osseus*, newly hatched larvae have adhesive pad on the head that allows them to adhere to the substrate or objects on the substrate. This organ is lost early in development. Sometimes hybridizes with *L. platyrhincus*.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Turns up frequently in the pet trade. ◆

Longnose gar
Lepisosteus osseus

FAMILY
Lepisosteidae

TAXONOMY
Lepisosteus osseus Linnaeus, 1758, eastern United States.

OTHER COMMON NAMES
English: Billfish, common gar pike, needlenose gar; French: Garpique longnez; German: Gemeiner Knochenhecht, Gemeiner Langschnäuziger, Langnasen-Knochenhecht; Spanish: Catán, gaspar picudo, pejelagarto.

PHYSICAL CHARACTERISTICS
Maximum total length about 6 ft (183.4 cm), weight of about 50 lb (22.7 kg). Has the longest snout and most elongate body shape of any gar species. Color pattern variable. As a juvenile, it has a lateral stripe that disappears in the adult.

DISTRIBUTION
Southern Quebec, Canada, south to Florida, United States, westward from the Great Lakes region to Montana, United States, and from Florida to northern Mexico. Reported as a fossil from Pleistocene deposits of Kansas and North Carolina, United States, although species identification of this fragmentary material is tenuous.

HABITAT
Normally inhabits quiet, weedy, shallow-water lake environments or large rivers. Typically freshwater, but occasionally enters brackish water along its coastal distribution, particularly in the southern United States. Can also survive for weeks in oxygen-poor stagnant ponds and canals by breathing air at the surface with its functional lung (vascularized swim bladder).

BEHAVIOR
Often lies motionless near the surface until prey swim within reach. With a quick sideways thrust of its sharply toothed bill, it impales the prey.

FEEDING ECOLOGY AND DIET
Voracious predators; by the time they reach about 1 in (2.6 cm) total length, feed primarily on other fishes. Also feed on decapods, insects, and other invertebrates. Young are cannibalistic, sometimes feeding on siblings 70% of their own length.

REPRODUCTIVE BIOLOGY
Lake-dwelling; often migrates up streams and rivers to spawn. Some also spawn in nearshore lake shallows. Eggs in a female 40 in (102 cm) long can number more than 36,000. Males mature at three or four years, females at six. Longevity appears to be sexually dimorphic.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Occasionally turns up in the pet trade. ◆

Shortnose gar
Lepisosteus platostomus

FAMILY
Lepisosteidae

TAXONOMY
Lepisosteus platostomus Rafinesque, 1820, type locality not specified but probably Mississippi River basin, United States.

OTHER COMMON NAMES
English: Duckbill garfish; Finnish: Pikkuluuhauki.

PHYSICAL CHARACTERISTICS
Maximum total length 34.6 in (88 cm). Has a reduced color pattern on the trunk region (i.e., spots are few and not as strong as in other *Lepisosteus* species) and two complete rows of premaxillary teeth.

DISTRIBUTION
Primarily within the low gradient regions of the Mississippi River basin in the United States, running from northeastern Texas north to Montana, east to Ohio, and south to Mississippi. It is absent from the Ozark plateau. Has been reported as a fossil from Kansas, but the material is too fragmentary to be reliably included in the species.

HABITAT
Quiet, sparsely planted backwater areas of rivers, lakes, and oxbows. Appears to be more tolerant of turbidity than most other gar species.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Feeds mainly on crayfishes, fishes, and aquatic insects.

REPRODUCTIVE BIOLOGY
Reaches sexual maturity at about three years of age. Spawning takes place in spring. Eggs are scattered in quiet, shallow, freshwater and hatch in about eight days. Young become active (and feed) about seven days after hatching.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Florida gar
Lepisosteus platyrhincus

FAMILY
Lepisosteidae

TAXONOMY
Lepisosteus platyrhincus DeKay, 1842, Florida, United States.

OTHER COMMON NAMES
English: Florida spotted gar; Finnish: Floridanluuhauki.

PHYSICAL CHARACTERISTICS
Maximum total length 52.4 in (133 cm). Has numerous dark brown spots covering the anterior body and head; spots similar to those of *L. oculatus*, but more prominent and darker on the dorsal surface of the head and body. Also distinguished from *L. oculatus* by the lack of plates on the ventral surface of the isthmus.

DISTRIBUTION
Florida and the lowlands of southern Georgia, United States. Reported from Pleistocene deposits of Florida based on fragmentary material, but material is too fragmentary to be reliably included in the species.

HABITAT
Quiet lowland streams and lakes with heavy vegetation and a mud-sand bottom. The rarity of records of this species in brackish or salt water may reflect a very limited tolerance to salinity.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Feeds primarily on fishes, but also on crustaceans and insects.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive habits; may interbreed with *L. oculatus* in the Apalachicola River drainage.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Turns up frequently in the pet trade.

Resources

Books

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Lance Grande, PhD

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Amiiformes
(Bowfins)

Class Actinopterygii
Order Amiiformes
Number of families 1

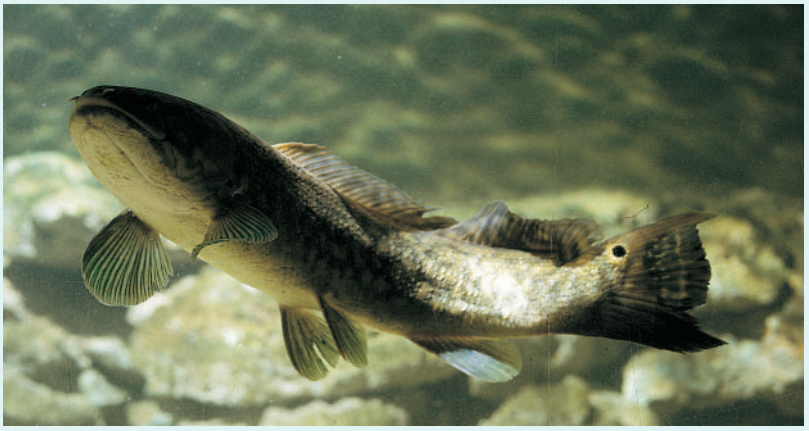

Photo: Bowfins (*Amia calva*) are found in lakes and slow moving rivers. (Photo by Tom McHugh/Shedd Aquarium/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Amiiformes (*sensu* Grande and Bemis, 1998) contains one extant family, Amiidae, and three extinct families, Caturidae, Liodesmidae, and Sinamiidae.

The family Amiidae is another of the so-called living fossil families. In other words, it is a relatively basal neopterygian group with an old history (late Jurassic to present day), a formerly diverse distribution (with numerous genera and species in the Jurassic through the Eocene), and only a single extant species. The bowfin (*Amia calva*) is the only living species remaining from the order Amiiformes.

The Amiidae is one of only five extant families of actinopterygian fishes outside of Teleostei. Consequently, it is a family of great interest to fish systematists and evolutionary biologists. Even its most basic relationships remain controversial (i.e., is Amiidae the living sister group to Teleostei, or to Lepisosteidae?). Although there is only a single species in the family today, a rich fossil record going back over 150 million years to the late Jurassic indicates that in the past the family contained many more species, and was morphologically diverse and geographically widespread. In their revision of the Amiidae, Grande and Bemis (1998) divided the family into four subfamilies: Amiinae, Vidalamiinae, Solnhofenamiinae, and Amiopsinae. Amiopsinae was an extinct group with five valid species (some marine, some freshwater) ranging in age from late Jurassic to late Cretaceous (about 150 million to 100 million years ago). The group is known only from fossil deposits of western Europe. Solnhofenamiinae is an extinct group containing a single valid species and is known from late Jurassic marine deposits of western Europe. Vidalamiinae is an extinct group containing five genera and eight valid species (some marine, some freshwater) ranging in age from at least the early Cretaceous to the early Eocene (about 135 million to 55 million years ago). The group is known from deposits located in western Europe, North America, eastern South America, and western Africa. Amiinae is a freshwater subfamily containing two valid genera and about 11 valid species. This subfamily ranges in age from at least the late Cretaceous (about 95 million years ago) through to the present. While the twenty-first century finds this family living only in North America, fossil members are widespread throughout the Northern Hemisphere.

Taxonomy is *Amia calva* Linnaeus, 1766, Charleston, South Carolina, United States.

Other common names: English: Blackfish, cottonfish, cypress trout, freshwater dogfish, grindle, grinnel, marshfish, mudfish, scaled ling, speckled cat; French: Choupique, poisson de marais.

Physical characteristics

The Amiidae are uniquely characterized by the condition of their caudal vertebral region. Most of the caudal centra are

Bowfin (*Amia calva*). (Illustration by Brian Cressman)

both solidly ossified and diplospondylous; in other words, the neural and haemal arches occur only on every other centrum rather than on every centrum. Like all halecomorphs, amiids have a peculiar double jaw articulation in which the jaw suspension bones articulate with the lower jaw at two separate places rather than one.

Amia calva is characterized, among living fishes, partly by its long, bow-shaped dorsal fin; hence the common name "bowfin." There are also several fossil species of bowfin (species in the genera *Amia* and *Cyclurus*) dating back as far as the late Cretaceous (about 65 million years ago). The living species reaches a total length of approximately 35.4 in (90 cm).

Distribution

The bowfin is restricted to eastern North America, inhabiting fresh waters over most of the eastern half of the continental United States, southern Ontario, and Quebec, Canada.

Habitat

The bowfin is known only from fresh waters. As an adult it generally inhabits swampy, sluggish water of vegetated bays of warm lakes and rivers. Young individuals are rarely seen after the postlarval schools break up, suggesting that they move into deeper water or dense vegetation.

Behavior

Amia calva is a very hardy species. These fishes can withstand high temperatures and breathe air at the surface if necessary. They are even known to estivate. Specimens have been documented as being out of water for 24 hours without apparent harm.

Feeding ecology and diet

Bowfins are voracious predators. At the small postlarval stages (e.g., under 4 in/10 cm) total length) this species feeds on small animals such as insects, insect larvae, ostracods, and other zooplankton. Once the fishes start to get larger than about 4 in (10 cm), other fishes become its primary diet. Adults are also known to eat decapods. Observations of aquarium specimens indicate that the bowfin is a sluggish, clumsy, stalking predator that uses scent as much as sight in stalking food, which it captures by means of sudden intake of water. Other than humans, natural predators of adult *Amia calva* are unknown.

Reproductive biology

Bowfins spawn in spring. The males move into shallow waters of lakes and rivers, where they prepare a circular nest in areas of heavy vegetation or under logs. Once a female is attracted into the nest, spawning takes place, and four or five batches of eggs are laid. The eggs are adhesive and stick to the bottom of the nest. Females can lay up to 64,000 eggs. The young hatch in eight to 10 days and, like gars, have an adhesive organ on the tip of the snout by which they remain attached to vegetation (or other objects on the bottom) for seven to nine days. Then the young form a compact school which is guarded by the males for several weeks.

Conservation status

Bowfins are not on the IUCN Red List and are currently quite common in areas of the southern United States.

Significance to humans

As with gars, bowfins are often considered to be pest fishes. They have little value as food fishes, and are of little commercial or recreational use. Yet they are important predators in some regions, controlling undesirable species.

Resources

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Lance Grande, PhD

Osteoglossiformes

(Bony tongues and relatives)

Class Actinopterygii
Order Osteoglossiformes
Number of families 6

Photo: Clown knifefish (*Chitala chitala*) as juveniles have stripes, but adults lose the stripes, and have ringed spots instead. (Photo by M. H. Sharp/ Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The osteoglossiformes are an unusual group of teleost fishes comprising about 220 species of freshwater fishes, most of which are in one African family, the Mormyridae (19 genera; 182 species). The other species are scattered about the continents and are generally considered to be relicts of a once more abundant group. Fossil records of the family Osteoglossidae indicate these fishes to be between 38 and 55 million years old. However, the present distribution of members of the Osteoglossidae family suggests that the group was present on Gondwana prior to Gondwana's fragmentation. Biogeographic evidence thus suggests a considerably greater age than the 55 million years inferred from the fossil record. Most osteoglossiformes have most of their teeth located on the tongue and on the roof of the mouth. They also have a caudal fin with 16 or fewer branched rays (most bony fishes have more), lack intermuscular bones on the back, and have cycloid scales with ornate microsculpturing. The intestine curls around to the left side of the esophagus rather than to the right as in most other bony fishes.

Six living families are recognized. The monotypic family Gymnarchidae (*Gymnarchus niloticus*) together with the Mormyridae, comprises the superfamily Mormyroidea; this group is considered the sister group of the Notopteroidea (family Notopteridae; four genera and eight species). The position of the three remaining families is somewhat uncertain. The Osteoglossidae comprise seven species (four genera) and the Pantodontidae but one. The phylogenetic position of the Hiodontidae (two species) is not very clear. The two species of this family have a similar ear–swim bladder connection as do the clupeomorph fishes.

Recent data indicate the presence of a group of mormyrid fishes of the genus *Brienomyrus* in Gabon of uncertain taxonomic status. Morphological, physiological (electric discharge), and molecular genetic data indicate these fishes represent a species flock. A comparable situation is known from the East African lakes Victoria, Malawi, and Tanganyika. A very limited number of riverine cichlid species adjusted to lacustrine conditions and have evolved into a species flock now comprising more than 200 species in each lake and dominating the fish fauna of these lakes.

Physical characteristics

The Mormyridae, the elephantfishes, are odd-looking fishes ranging from 1.6 in to 5 ft (4 cm to 1.5 m) in length. The head morphology varies considerably related to feeding specializations: some species possess prolonged heads, others trunklike snouts or appendages on the lower jaw, hence the common name. The tail is often deeply forked and the caudal peduncle very narrow. The skin is thick and of high electrical resistance; all species indeed are weakly electric. The electric organ is located in the caudal peduncle. Larvae possess a larval electric organ in the lateral muscle. The electric field set up around the fish is used for electrolocation and electrocommunication. Related to this sensory modality is the enlarged cerebellum; thus brain volume, relative to body size, is roughly the same size as that of humans. Male elephantfishes in most species can be distinguished from females by the lobed, enlarged front part of the anal fin. The sperm of mormyrids lacks flagellum. In the remaining osteoglossiform fishes, sexual dimorphism is not very pronounced or lacking.

Gymnarchus niloticus, the only species of the family Gymnarchidae, can reach 5 ft (1.5 m) in length. It possesses a long snout and a long dorsal fin used for locomotion; the anal, caudal, and pelvic fins are absent. The fish produces sinusoidal weakly electric discharges.

The Peter's elephantnose (*Gnathonemus petersii*) normally emits 800 electrical impulses per minute. (Photo by Wally and Burkard Kahl. Reproduced by permission.)

The eight species of knifefishes of the family Notopteridae have long, strongly compressed bodies tapering to a point. The long anal fin extends from just behind the head to the tiny caudal fin, which it joins. The dorsal fin, which is absent from *Xenomystus nigri*, is small and featherlike, so these fishes are commonly called featherbacks. The swim bladder is connected to the gut and is used for air breathing. The species of the African subfamily Xenomystinae, genera *Xenomystus* and *Papyrocranus*, possess cutaneous electroreceptors. Knifefishes range from 7.9 in (20 cm) in length (in *Xenomystus nigri*) up to 5 ft (1.5 m) (in *Chitala lopis*, the giant featherback).

Species of the family Osteoglossidae, the bony tongues, have heavy, elongate bodies covered with large scales. The dorsal and anal fins are long and placed on the rear part of the body. All these fishes can apparently breathe air with their lunglike swim bladders. *Arapaima gigas* can reach lengths of about 14.7 ft (4.5 m); other species attain lengths of about 3.3 ft (1 m).

The African freshwater butterflyfish, the only species of the family Pantodontidae, reach 3.9 in (10 cm) in length. The fishes possess a large gape and a straight dorsal profile. The pelvic fins with the prolonged fin rays are located under the greatly enlarged, winglike pectorals. The swim bladder can act as an air-breathing organ.

The two species of the family Hiodontidae, the mooneye (*Hiodon tergisus*) and the goldeye (*H. alosoides*), superficially resemble clupeid fishes. Their most distinctive external features are their large eyes, which have bright gold irises (goldeye) or gold/silver irises (mooneye). Goldeyes have only rods in their retinas and are known to feed mostly at night.

Distribution

Elephantfishes occur all over tropical Africa. The highest diversity is found in the Congo River basin, where mormyrids comprise about 20% of the total number of about 600 fish species. *Gymnarchus niloticus* is found in all large rivers of the Sahelo/Sudanean region in Africa.

African knifefishes inhabit coastal streams in West Africa (*Xenomystus nigri* and *Papyrocranus afer*), or the Congo basin (*P. congoensis*). The Asian knifefishes are found in the Indus, Ganges-Brahmaputra, and Mahanadi River basins in India (*Chitala chitala*), in Indonesia, Malaysia, and Thailand (*Chitala lopis*), and in Laos, Thailand, Cambodia, and Vietnam (*Chitala ornata*). *Notopterus notopterus* is very widely distributed, inhabiting rivers in India, Indochina, Thailand, Malaysia, and Indonesia.

The three South American bony tongues are either restricted to the Rio Negro (*Osteoglossum ferreira*), or occur in the Amazon River system and French Guiana (*Arapaima gigas* and *O. bicirrhosum*). *Heterotis niloticus* occurs in Africa in all river basins of the Sahelo/Sudanian region. The Asian bony tongue (*Scleropages formosus*) is native to Indonesia, Malaysia, Thailand, Cambodia, and Vietnam. *S. jardini* is found in New Guinea and Northern Australia; *S. leichardti* is restricted to northeastern Australia.

Pantodon buchholzi, the only representative of the family Pantodontidae, occurs in various rivers of central and West Africa.

The two species of *Hiodon* are found in the central part of North America, with *H. alosoides* being more widely distributed than *H. tergisus*.

Habitat

African elephantfishes are mainly riverine species and rarely occur in lakes. They are pelagic, midwater, or bottom-oriented fishes. The knifefishes inhabit stagnant backwaters of the large rivers, and are sometimes found in lakes; the smaller species prefer habitats with dense vegetation. Large bony tongues are found in open, slow-moving, or stagnant water and are surface-oriented hunters. *Pantodon buchholzi* prefers surface water of habitats with stagnant water. *Hiodon alosoides* lives in turbid waters in large lakes and muddy rivers, occasionally in swift current. *H. tergisus* is usually found in the clear waters of large lakes and streams.

Behavior

Elephantfishes are nocturnal, often hiding during the day in dense vegetation or under other kinds of cover. Aquarists have long admired mormyrids for their learning abilities and the fact that many species engage in apparent "play" behavior consisting of batting around small objects, including air bubbles, with the head. They usually swim slowly with their body rigid, presumably to avoid distorting the electrical field they are generating. The electric field is used for electrolocation and electrocommunication. The frequency of the electric signals can be modified to communicate with other fish, and thus can be used in courtship, aggressive behavior, and other intraspecific encounters. Because each species has its own set of electrical patterns, recognition and avoidance of other species is also possible. Mormyrids possess a well-developed sense of hearing; a part of the small swim bladder is in contact with the inner ear. Mormyrids use acoustic signals during courtship behavior. *Gymnarchus niloticus*, the

close relative of the mormyrids, produces sinusoidal electrical discharges (the elephantfishes produce pulse-type discharges); this slow moving fish also uses its discharge for electrolocation. Knifefishes generally remain quietly in cover during daytime, but come out to prey in the evening. Bony tongued fishes are active during the day, spending most of the time patrolling very close to the surface. From aquaculture and aquarium observations, it has been deduced that the Australian spotted barramundi (*Scleropages leichardti*) can withstand water temperatures of between 44.6 and 104°F (7 and 40°C). During the summer, when surface temperatures exceed 87.8°F (31°C) in their natural habitat, surface cruising ceases and the fish remain in deeper, cooler areas. *Pantodon buchholzi* is a slow-moving fish of surface waters; it can jump out of the water and has been observed gliding over 13.1–16.4 ft (4–5 m). The pronounced tapetum lucidum of the two *Hiodon* species enables these fishes to hunt effectively at night.

Feeding ecology and diet

The mormyrid fishes eat various kinds of zooplankton or feed on a variety of benthic organisms such as insect larvae, crustaceans, oligochaets, and snails. The species with the long snouts find their prey in holes and crevices. Large *Mormyrops* species are piscivorous. Elephantfishes themselves are eaten by the large predator *Gymnarchus niloticus* (who also feeds on other fishes) and large piscivorous catfishes. Smaller knifefishes feed on insect larvae, crustaceans, worms, and snails; the larger species are mainly piscivorous. The bony tongues are midwater and surface feeders. Species of the genus *Osteoglossum* and *Scleropages* are carnivorous, feeding in roughly equal measure upon smaller fishes and terrestrial insects. While large specimens of both are known to take small terrestrial vertebrates opportunistically, these items do not constitute a significant portion of their diet in nature. The large *Arapaima gigas* prefers fishes. *Heterotis niloticus* has its fourth gill arch modified into a spiral-shaped filtering apparatus. This organ secretes mucus in which phytoplankton and bits of organic matter are trapped and then swallowed. The surface-oriented *Pantodon buchholzi* lives on crustaceans, insects, and small fishes. The two species of the family Hiodontidae feed on a variety of prey, including aquatic insects, crustaceans, mollusks, small fishes, frogs, shrews, and mice. They are preyed upon by birds, some mammals, and other fishes.

Reproductive biology

Most osteoglossiform fishes breed during the rainy season. Experimental studies with elephantfishes have shown that gonad maturation is triggered by decreasing water conductivity. About nine species have been bred in captivity. Parental care in the male is found in *Pollimyrus isidori*; the eggs are transported after oviposition by the male into the nest of about 2 in (5 cm) in diameter, generally made from plant material. After hatching (three days after fertilization) the male guards the embryos until the beginning of exogenous feeding (on days 13–14) and also during the larval period. Courtship behavior is characterized by acoustic and electrical behavior. Species of the genus *Stomatorhinus* probably also show parental care. The remaining species bred so far (*Petrocephalus soudanensis*, *Brienomyrus brachyistius*, *Marcusenius* sp., *Mormyrus rume proboscirostris*, *Mormyrus* sp., *Hippopotamyrus pictus*, *Campylomormyrus cassaicus*, and *C. phantasticus*) do not show parental care.

African arawanas or "bony tongues" (*Heterotis niloticus*) live in nothern and western Africa, in the Nile, Senegal, Gambia and Niger Rivers. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

Egg size ranges between 0.07 in (1.8 mm) in *P. soudanensis*) and 0.12 in (3 mm) in *H. pictus*. Eggs number between a few hundred in *P. isidori*, and more than a thousand in *C. cassaicus*. Spawning intervals range between a few days in *P. isidori* and several weeks in most other species.

Gymnarchus niloticus breeds in swamps during the high-water season. Prior to spawning, these fishes construct a floating nest of plant fibers in which the thousand or so eggs, each about 0.39 in (10 mm) in diameter, are laid. The newly hatched young have long gill filaments and an elongate yolk sac. They come to the surface for air. Young fishes feed on insects and other invertebrates.

Reproduction in knifefishes is not well known. *Xenomystus nigri* females lay 150–200 eggs of 0.08 in (2 mm) diameter; in *Notopterus notopterus*, eggs (1,000–3,000) are deposited in small clumps on submerged vegetation. *Chitala chitala* lays eggs on a stake or stump of wood, the male fans them with his tail and guards them against predators. *Arapaima gigas* males build a nest about 6 in (15 cm) deep and 20 in (50 cm) wide in sandy bottoms at the end of the dry season; the large eggs and young are guarded by the male and occasionally by the female. Parental care lasts up to 14 weeks. The two *Osteoglossum* species are male mouth brooders. The large eggs (about 0.6 in/16 mm diameter) are incubated for 50–60 days. At release, the juveniles measure 3.1–3.9 in (8–10 cm).

The *Scleropages* species are female mouth brooders. *S. leichardti* incubates 70–200 eggs about 0.4 in (10 mm) in diameter. Spawning occurs in small ponds during spring, when water temperatures rise to 68–73.4°F (20–23°C). Hatching takes place between one and two weeks after spawning; the embryos with their large yolk sac are about 0.6 in (15 mm) long. After the total incubation period of five to six weeks, the juveniles are released at a total length of about 1.4 in (35 mm). During a three-day period, the female shows a "release-and-recall" behavior. When the young become independent of the female, they take up territories around the edge of the pond. *Heterotis niloticus* is a nest builder, breeding in still waters close

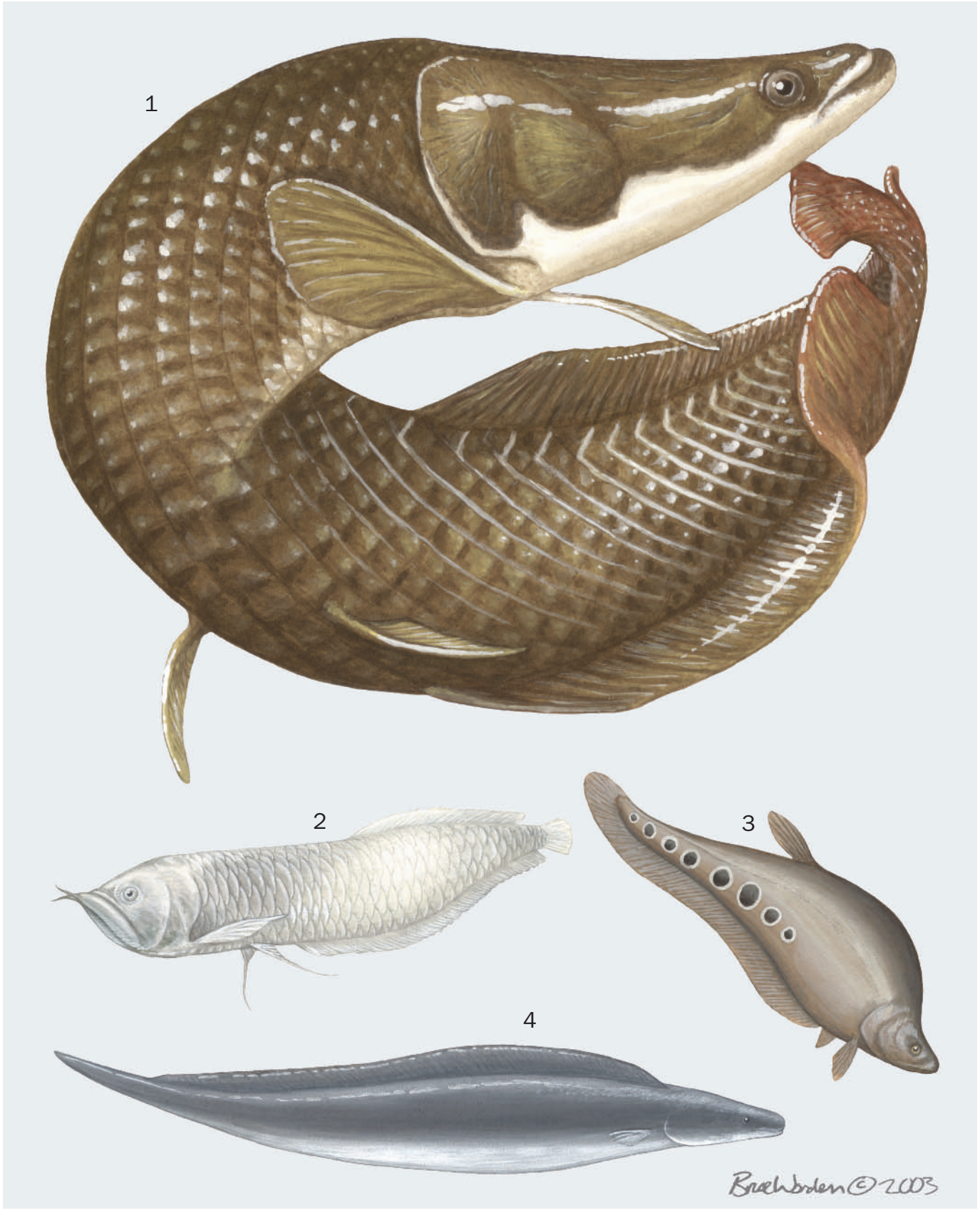
to the river, and excavating a nest some 3.9 ft (1.2 m) in diameter with thick walls of vegetation and mud. Within this nest, eggs about 0.1 in (2.5 mm) in diameter are laid; protected by the parents; they hatch in two days. The newly hatched embryos have external gills. *Pantodon buchholzi* has a prolonged spawning season, spawning 80–200 small buoyant eggs every day; the small embryos hatch after 36 hours. Goldeye (*Hiodon alosoides*) spawn in late spring on gravelly shallows of tributary streams. Their eggs are about 0.16 in (4 mm) in diameter, and are semibuoyant even after hatching, as the oil globule in the yolk buoys up the newly hatched 0.3 in (7 mm) embryo.

Conservation status

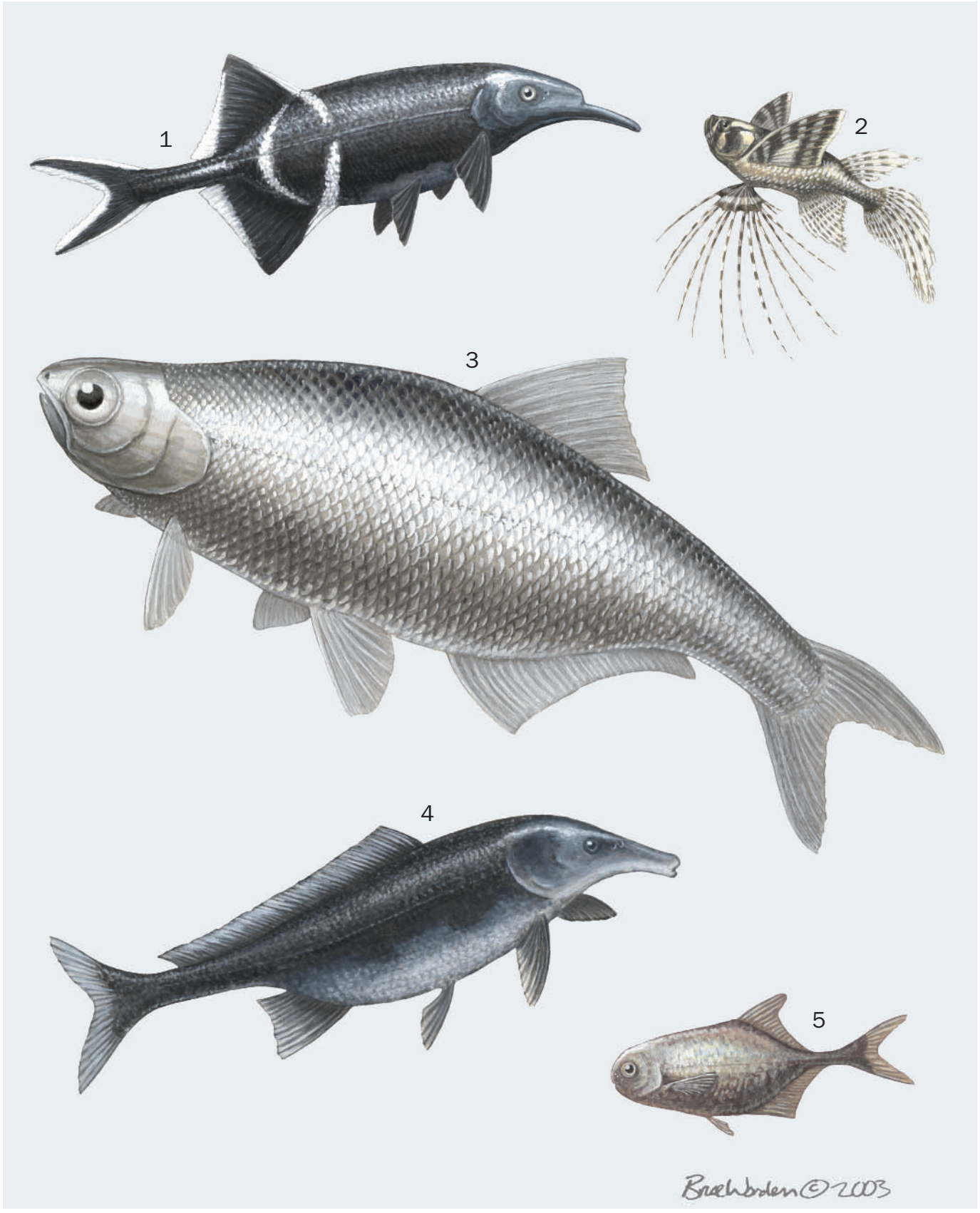
Four species are listed by the IUCN: *Arapaima gigas* is listed as Data Deficient; *Chitala blanci* is listed as Lower Risk/Near Threatened; *Scleropages formosus* is listed as Endangered; and *Scleropages leichardti* is listed as Lower Risk/Near Threatened. *Scleropages formosus* is also included on Appendix I of CITES, as a result of which international trade is banned (CITES Appendix I). For *Arapaima gigas*, international trade is restricted (CITES Appendix II).

Significance to humans

Most osteoglossiform fishes, particularly the larger species, are economically important food fishes. Even many of the medium-sized African elephantfishes, which measure approximately 7.9–23.6 in (20 to 60 cm) in length, are regularly fished for food. Some of the larger osteoglossiforms are used in aquaculture, including *Arapaima gigas*; *Scleropages leichardti* and *S. jardini*; *Heterotis niloticus*; *Chitala blanci* and *C. chitala*; and *Notopterus notopterus*. The larger species are important as food fishes, as well as for exhibition in public aquaria. The various color breeds of *Scleropages formosus* are favored as ornamental fishes in Asia. The elephantfish, *Gnathonemus petersii*, is a well-known species in the international aquarium trade. Several species of the weakly electric mormyrids are intensively studied by scientists.



1. Arapaima (*Arapaima gigas*); 2. Arawana (*Osteoglossum bicirrhosum*); 3. Clown knifefish (*Chitala chitala*); 4. Aba-aba (*Gymnarchus niloticus*). (Illustration by Bruce Worden)



1. Elephantnose fish (*Gnathonemus petersii*); 2. Freshwater butterflyfish (*Pantodon buchholzi*); 3. Mooneye (*Hiodon tergisus*); 4. *Mormyrus rume proboscirostris*; 5. Elephantfish (*Pollimyrus isidori*). (Illustration by Bruce Worden)

Species accounts

Aba-aba
Gymnarchus niloticus

FAMILY
Gymnarchidae

TAXONOMY
Gymnarchus niloticus Cuvier, 1829, Nile River.

OTHER COMMON NAMES
German: Nilhecht.

PHYSICAL CHARACTERISTICS
Maximum size 5.48 ft (1.67 m) at 40.8 lb (18.5 kg). Heavy elongate fishes covered with small scales. Have long anal fin tapering in a short caudal appendage, lack dorsal, pelvic, and caudal fins. Caudal part can regenerate after injury. Anal fin used for propulsion. Weakly electric fish.

DISTRIBUTION
Large rivers and back waters of the Sahelo and Sudanian regions of Africa

HABITAT
Back waters with slow-moving or stagnant water, vegetation, and various kinds of cover.

BEHAVIOR
Nocturnal; hides during daytime. Very aggressive towards conspecifics. Weakly electric discharges of the sinusoidal type used for electrolocation.

FEEDING ECOLOGY AND DIET
Piscivorous, ecology not well known.

REPRODUCTIVE BIOLOGY
Breeds in swamps during the high-water season. Prior to spawning, a floating nest of plant fibers is created, most probably by the male. 1,000 or so eggs, each about 0.16 in (4 mm) in diameter, are laid in the nest. The newly hatched young have long gill filaments and an elongate yolk sac. They come to the surface for air. Young fishes feed on insects and other invertebrates. Parental males defend the nest very aggressively and do not hesitate to attack and bite human intruders. It is quite common to see fishermen in West Africa with the distinctive half moon–shaped scars left by an Aba-aba attack.

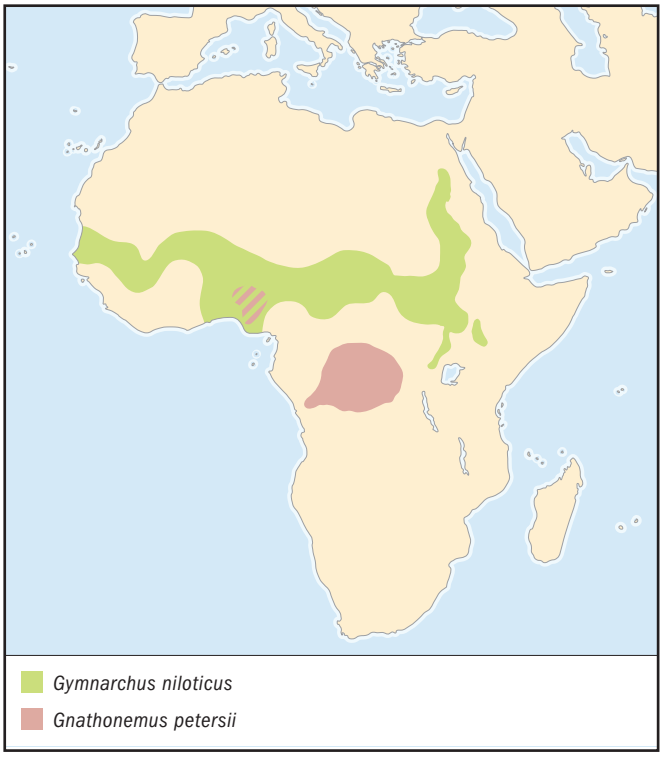
CONSERVATION STATUS
Not listed by the IUCN.

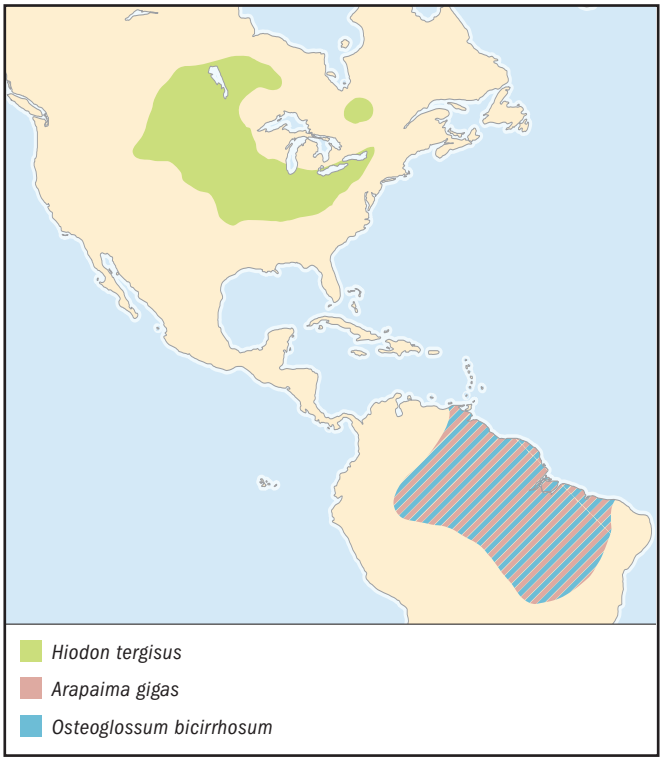
SIGNIFICANCE TO HUMANS
Very important food fish. Risk of overexploitation due to low reproductive capacity (low number of fry). ◆

Mooneye
Hiodon tergisus

FAMILY
Hiodontidae

TAXONOMY
Hiodon tergisus LeSueur, 1818, Lake Erie at Buffalo, New York, and Ohio River at Pittsburgh, Pennsylvania, United States.





OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum size 17 in (43 cm). Resembles clupeid or cyprinid fishes with large eyes and large oblique gape. The tapetum lucidum of the retina gives the silvery appearance of the eye.

DISTRIBUTION
St. Lawrence River and the Great Lakes (except Lake Superior) in Canada and United States; Mississippi River in the United States, Hudson Bay basins from Quebec to Alberta in Canada, and south to Gulf of Mexico. Gulf slope drainages from Mobile Bay in Alabama to Lake Pontchartrain in Louisiana.

HABITAT
Deep pools and backwaters of medium to large rivers, lakes, and impoundments; prefers clear water.

BEHAVIOR
The specialized eyes allow the fishes to forage at low light intensities.

FEEDING ECOLOGY AND DIET
Insects, insect larvae, and small fishes.

REPRODUCTIVE BIOLOGY
Reproduction biology probably similar to that of the related species *H. alosoides*. Spawning occurs in late spring on gravelly shallows of tributary streams. Eggs are about 0.16 in (4 mm) in diameter and are semibuoyant due to oil globules.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The species is locally exploited for food. ◆

Elephantnose fish
Gnathonemus petersii

FAMILY
Mormyridae

TAXONOMY
Gnathonemus petersii Günther, 1862, "Old Calabar, Westafrika."

OTHER COMMON NAMES
English: Peter's elephantnose; German: Tapirfisch, Elefanten-Rüsselfisch, Spitzbartfisch.

PHYSICAL CHARACTERISTICS
Maximum length 9.8 in (25 cm). Slender, laterally compressed fish with long dorsal and anal fin located at the rear part of the body. Narrow caudal peduncle houses the weakly electric organ. Caudal fin deeply forked. Body coloration dark brown to black. Two whitish transversal bands at the beginning and in the middle of dorsal and anal fins. Chin barbel on lower jaw.

DISTRIBUTION
West Africa from Niger to Congo River basins. Limited to the Lower Niger, in the Ogun, in the Cross River Basin and in the Upper Chari.

HABITAT
Habitat not very well known, but probably slow-moving waters of large rivers.

BEHAVIOR
Social and nocturnal. Often occurs in large schools. Weakly electric discharges of the pulse type used for electrocommunication. Captive animals appear to have a complex social structure, with a nonlinear "peck order."

FEEDING ECOLOGY AND DIET
Bottom-oriented, feeds on invertebrates of soft substrate.

REPRODUCTIVE BIOLOGY
Not known. Probably spawns during the rainy season.

CONSERVATION STATUS
Not listed by the IUCN.

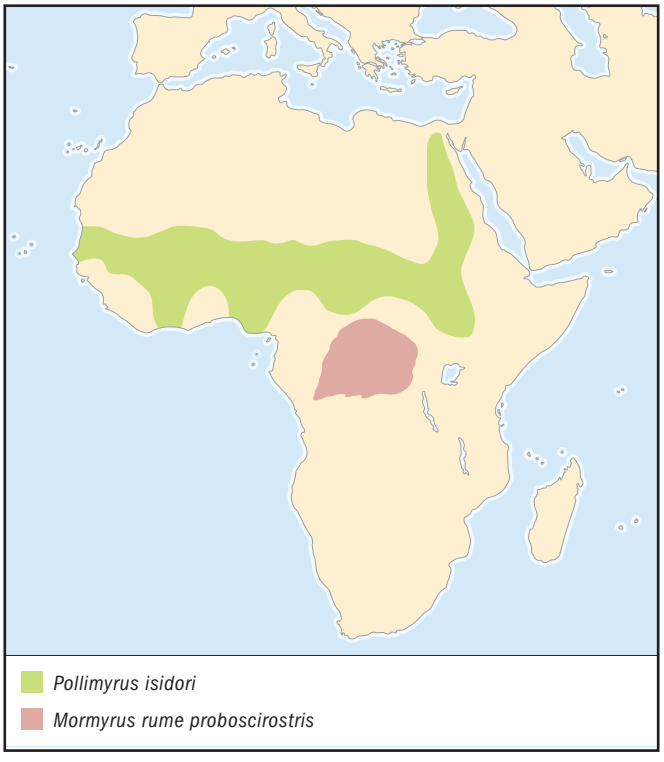
SIGNIFICANCE TO HUMANS
Most important mormyrid species in the international fish trade. Known to aquarists for their "play" behavior. Often used in scientific studies concerning neuroanatomy, physiology, and behavior. ◆

No common name
Mormyrus rume proboscirostris

FAMILY
Mormyridae

TAXONOMY
Mormyrus rume proboscirostris Boulenger, 1898, "Upoto" Upper Congo.

OTHER COMMON NAMES
Chokwe (Angola): Sosha.



PHYSICAL CHARACTERISTICS
Maximum length about 13.7 in (35 cm). Elongate fishes with very long dorsal fin, short anal, and forked caudal fin. Snout prolonged and curved downward, dolphinlike. Electric organ in adults in the caudal peduncle; in the lateral muscle of young fish a larval electric organ is found. Mormyrus is the only mormyrid genus whose members produce weakly electric discharges of up to 30 V, which can be felt by touching the caudal peduncle of the fish. Body coloration dark gray.

DISTRIBUTION
Congo River basin in Africa.

HABITAT
Not known.

BEHAVIOR
Very active both day and night. Very social fish, however with many aggressive interactions that can cause death of subordinate specimens.

FEEDING ECOLOGY AND DIET
Feeds on insect larvae, crustaceans, and mollusks, as well as small fishes. Produces fine jets of water with the tubular mouth in search for prey in the substrate.

REPRODUCTIVE BIOLOGY
Reproduction occurs during the high-water season. Gonad maturation can be provoked experimentally by decreasing conductivity for several weeks. During each fractional spawning event several hundred eggs of 0.1 in (2.5 mm) in diameter are deposited. Hatching on day three. Exogenous feeding starts on day 10–11. Spawning intervals three to four weeks. No parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
All *Mormyrus* species are economically important as food fishes. ◆

Elephantfish
Pollimyrus isidori

FAMILY
Mormyridae

TAXONOMY
Pollimyrus isidori Valenciennes, 1847, "Westafrika."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum length 3.94 in (10 cm). Broad, laterally compressed fish with long dorsal and anal fins located at the rear part of the body. Slightly subterminal mouth. Weakly electric organ found in the narrow caudal peduncle. Larval electric organ in the lateral muscle of larvae up to 1 in (25 mm) long. Body coloration uniform gray and black.

DISTRIBUTION
Nile River, Upper and Middle Niger, Chari, and Lagone River systems, including Lake Chad. Disjunctly distributed in the coastal rivers of West Africa between the Niger and the Sénégal.

HABITAT
Slow-moving water and back waters of rivers; lakes.

BEHAVIOR
Nocturnal and territorial. Males occupy territories of 3.3–9.8 sq ft (1–3 sq m). Pronounced acoustic signaling during courtship behavior.

FEEDING ECOLOGY AND DIET
Insect larvae, crustaceans, and small mollusks.

REPRODUCTIVE BIOLOGY
Reproduction occurs during the rainy season. Parental care in the male. Thirty to 200 eggs 0.1 in/2.5 mm in diameter are deposited in a nest of plant material. Free embryos and larvae are also guarded; exogenous feeding starts on days 13–14. Spawning intervals five to 20 days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Best-studied mormyrid fish in science concerning reproductive biology. ◆

Clown knifefish
Chitala chitala

FAMILY
Notopteridae

TAXONOMY
Chitala chitala Hamilton, 1822, type locality unknown (probably India or East Indies).

OTHER COMMON NAMES
English: Clown featherback; German: Indischer Messerfisch.

PHYSICAL CHARACTERISTICS
Up to 31.5–35.4 in (80–90 cm) long. Strongly compressed, tapering to a point. Very long anal fin continuous with the caudal, small dorsal fin. Dorsal profile is markedly convex. Small pelvic fins unite together at their base.

DISTRIBUTION
Indus, Ganges, Brahamaputra, and Mahandi River basins in India.

HABITAT
Rivers, canals, reservoirs, and ponds.

BEHAVIOR
Generally remains quietly in cover during daytime, but comes out to prey at night.

FEEDING ECOLOGY AND DIET
Aquatic insects, mollusks, shrimps, and small fishes.

REPRODUCTIVE BIOLOGY
Spawns once a year during May to August. Eggs usually laid on wooden substrate, male fans them with tail and keeps them aerated and silt free. Eggs are guarded against small catfishes and other predators. Embryos hatch after one week and are guarded by the male for some days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Moderately important food and game fishes also used in aquaculture. Large specimens are often exhibited in public aquaria. ◆

Arapaima
Arapaima gigas

FAMILY
Osteoglossidae

TAXONOMY
Arapaima gigas Schinz, 1822, probably Amazon River.

OTHER COMMON NAMES
English: Pirarucu; German: Paiche; Spanish: Paíche; Portuguese: Piracuçu.

PHYSICAL CHARACTERISTICS
Heavy elongate fishes with large, ornate scales. One of the largest freshwater fishes, reaching 15 ft (4.5 m) in length and 441 lb (200 kg). Pelvic and unpaired fins located posteriorly.

DISTRIBUTION
Amazon River system and French Guiana.

HABITAT
Midwater fishes found in open, slow-moving, or stagnant water.

BEHAVIOR
Slow-moving, air-breathing fishes that surface every 10–20 minutes. This behavior makes it an accessible target for harpoon fishermen. Sometimes aggressive toward conspecifics.

FEEDING ECOLOGY AND DIET
Swallow fish and other large prey. The diet also includes heavily armored loricariid catfishes. Ecology in general not well studied.

REPRODUCTIVE BIOLOGY
Breed at the end of the dry season. Male builds nest about 6 in (15 cm) deep and 19.7 in (50 cm) wide in sandy bottoms at the end of the dry season. Large eggs and young are guarded by the male and occasionally by the female. Parental care lasts up to 14 weeks.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN. Heavily overfished. The unsustainable and environmentally destructive practice of fishing for this species using dynamite during the breeding season has resulted in the loss of breeding pairs and their fry. This practice is one of the chief reasons for the dramatic decline of this species in western Amazonia. International trade restricted; listed on Appendix II of CITES.

SIGNIFICANCE TO HUMANS
One of the most important food and game fishes of Amazonia. Also used in aquaculture. Popular fish in public aquaria. ◆

Arawana
Osteoglossum bicirrhosum

FAMILY
Osteoglossidae

TAXONOMY
Osteoglossum bicirrhosum Cuvier, 1829, Amazon River.

OTHER COMMON NAMES
English: Silver aruana, aruana; German: Arabuana, Gabelbart.

PHYSICAL CHARACTERISTICS
Maximum size 3.3 ft (1 m). Large-scaled, elongate fishes, laterally compressed with straight dorsal provile and large gape. Very long anal and dorsal fins nearly joining the caudal fin. Prominent barbels at the tip of the chin.

DISTRIBUTION
Amazon River system and French Guiana.

HABITAT
Surface-orientated, live in open, slow-moving or stagnant water, preferably at the shore zone.

BEHAVIOR
Day active, spends most of the day patrolling very close to the surface.

FEEDING ECOLOGY AND DIET
Omnivorous, mainly eat invertebrates, or fishes to a lower percentage. Frequently jump out of the water to seize small vertebrates and large (particularly terrestrial) insects.

REPRODUCTIVE BIOLOGY
Reproduction takes place at the beginning of the floods, in general in December and January. About 200 large eggs 0.63 in (16 mm) in diameter are incubated in the males' mouth for 50–60 days. When released, juveniles are 3.15–3.93 in (8–10 cm) long.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An important food fish of Amazonia. Of special value in caboclo (person of mixed Brazilian, Indian, European, or African ancestry) folklore because it is one of the few species that women are allowed to eat postpartum; other species, especially catfishes, are thought to cause inflammation if eaten in times of illness and recovery. ◆

Freshwater butterflyfish
Pantodon buchholzi

FAMILY
Pantodontidae

TAXONOMY
Pantodon buchholzi Peters, 1877, Victoria River, Cameroon.

OTHER COMMON NAMES
French: Poísson papillon; German: Schmetterlingsfisch.

PHYSICAL CHARACTERISTICS
Small (up to 3.94 in/10 cm), surface-oriented fishes with straight dorsal profile and large, winglike pectorals; prolongated fin rays on the pelvic fins. Upper part of the body olive, ventral part silvery yellow amplified with red.

DISTRIBUTION
Lower Niger, Lake Chad, Cameroon, Ogooué, Congo River basin, and Upper Zambezi of Africa. A relict population might be present in Sierra Leone in Western Africa.

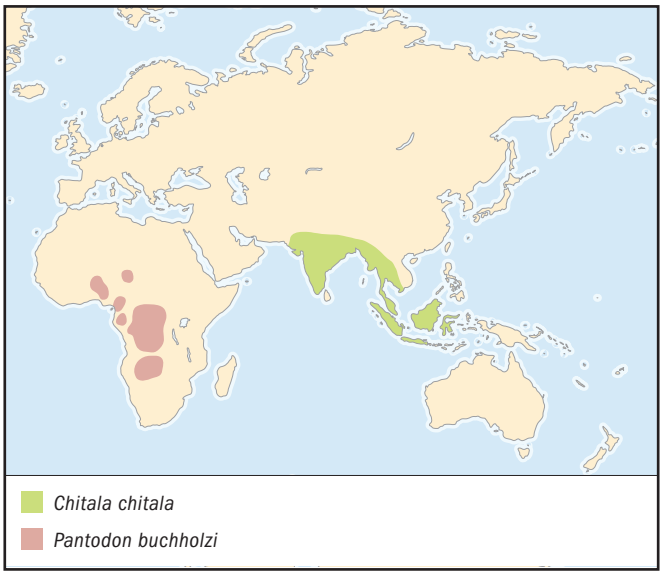
HABITAT
Surface water of habitats with stagnant water.

BEHAVIOR
Lives in schools underneath surface. Can jump out of the water for feeding or to escape predators. While this species has been observed gliding at distances between 13.1–16.4 ft (4–5 m), and even over 49.2 ft (15 m), this behavior needs to be documented and is highly controversial. The anatomy of the pectoral and ventral fins in this species display none of the anatomical modifications that would allow it to make long glides, nor does it possess the sort of hypertrophied pectoral musculature that permits powered flight.

FEEDING ECOLOGY AND DIET
Crustaceans, insects, and small fishes.

REPRODUCTIVE BIOLOGY
Prolonged spawning season. Spawning occurs preferably at night. Between 80–200 buoyant eggs, 0.12 in (3 mm) in diameter, are laid each night. The embryos hatch after 36 hours at 78.8°F (26°C) and are 0.43 in (11 mm) long. Raising is not easy as the fry need live food near the surface. Growth is rather quick; after one year individuals can reach 0.39 in (10 cm) in length and can begin to spawn.

CONSERVATION STATUS
Not listed by the IUCN.



SIGNIFICANCE TO HUMANS
None known.

Resources

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Frank Kirschbaum, PhD

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Elopiformes
(Ladyfish and tarpon)

Class Actinopterygii
Order Elopiformes
Number of families 2

Photo: Ladyfish (*Elops saurus*) inhabit shallow marine waters from Cape Cod to Brazil. (Photo by Garold W. Sneegas. Reproduced by permission.)

Evolution and systematics

Tarpon, along with bonefish and ladyfish, are primitive fishes, and while tarpon and ladyfish are considered to be more closely related to each other than to any other elopomorph group, their distinct lineages extend more than 100 million years back in the fossil record. The structure of the skull, fin placement, and large thick scales are characteristic of ancient fishes.

Tarpon and ladyfish are united by the common possession of a leptocephalus larvae and a variety of primitive features. The leptocephalus larvae is shared with a diverse group of other elopomorph fishes including the eels; however, the leptocephalus larvae of tarpon and ladyfish are the smallest of all leptocephali and possess a forked tail. Leptocephali of some albuliformes also have a forked tail.

The order Elopiformes contains two families: the Elopidae and the Megalopidae. The family Megalopidae contains the single genus *Megalops*. Two species of tarpon exist worldwide. The Atlantic tarpon occurs in the eastern and western Atlantic, and the oxeye tarpon occurs in the Indian and Pacific oceans. Morphologically the two species are quite similar; however, the Atlantic tarpon reaches a much larger size and can exceed 220 lb (100 kg) and a length of over 6.6 ft (2 m). The oxeye tarpon is smaller and seldom exceeds 3.3 ft (1 m).

The family Elopidae contains the single genus *Elops*, which occurs worldwide. As many as six morphologically similar species of *Elops* are thought to exist. The genus is in need of revision, and the total number of species is unclear.

Physical characteristics

These are silver, elongate herring-like fishes with large upturned mouths, large eyes, and deeply forked tails. An important structural character is the presence of a long, bony gular plate between the branches of the lower jaw, a feature that the ladyfish shares with the tarpon but not with herring.

Distribution

The Megalopidae and Elopidae occur worldwide in tropical and subtropical seas.

Habitat

Tarpon and ladyfish are coastal in habitat and often occur in estuarine waters. Both tarpon and ladyfish are quite tolerant of low salinities. Tarpon commonly enter freshwater and often travel far up freshwater rivers and enter lakes far from sea.

Behavior

Tarpon and ladyfish are pelagic predators that feed principally on mid-water prey. Both have small sandpaper-like teeth, and their prey is swallowed whole. They often occur in large schools in shallow coastal and inshore waters.

Feeding ecology and diet

Small tarpon feed predominantly on cyclopoid copepods, fishes, caridean shrimp, and mosquito larvae. No detailed studies have examined the feeding habits of large tarpon, but anecdotal information suggests that a wide variety of fishes are consumed. Ladyfish feed principally in midwater on pelagic prey. Feeding is mainly on fish, but decapod crustaceans also are consumed.

Ladyfish are probably preyed upon by a wide variety of inshore predators including sharks, porpoises, snook, and tarpon. They are occasionally used as bait by recreational anglers for tarpon and other species. Juvenile tarpon are also likely preyed upon by a variety of species such as gar, snook, and larger tarpon. Because juvenile tarpon are most often found in poorly oxygenated waters, they are probably vulnerable to a more limited suite of predators than ladyfish. Large tarpon are preyed upon only by large coastal sharks including bull sharks and hammerheads.

An Atlantic tarpon (*Megalops atlanticus*) with a school of silversides in the Grand Caymans. (Photo by Animals Animals ©Clay Wiseman. Reproduced by permission.)

Reproductive biology

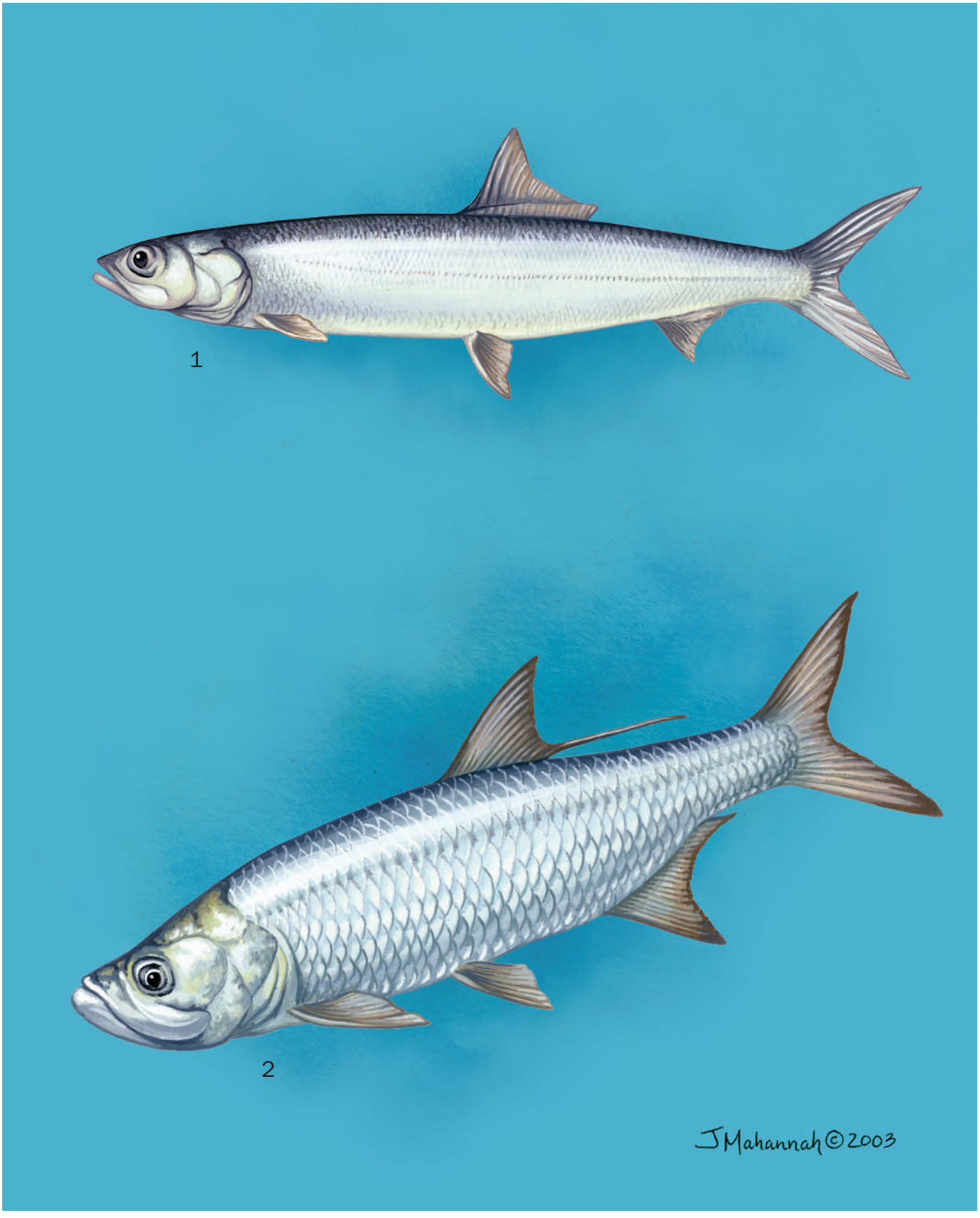
Both tarpon and ladyfish spawn offshore in high salinity oceanic waters. Precise spawning areas are unknown, and fertilized eggs are undescribed. Tarpon and ladyfish are broadcast spawners that produce large numbers of buoyant eggs that float in the surface waters of the ocean. The eggs hatch into the distinctive leptocephalus larvae characterized by an elongate, laterally compressed body consisting principally of an acellular mucinous material, large well-developed eyes, and large fang-like teeth. Larvae of tarpon and ladyfish reach a length of from 1.0 to 2.0 in (25–50 mm) before metamorphosis. Metamorphosis occurs as the larvae enter coastal waters and pass through inlets into the inshore waters where juveniles are found. Recruitment of tarpon through inlets appears to be pulsed and related to storm events.

Conservation status

Tarpon and ladyfish are abundant, and there is no evidence that stocks of these species have been depleted by overfishing. It is unknown to what extent habitat loss has affected stocks.

Significance to humans

Tarpon support important recreational fisheries in Florida and the Caribbean. Ladyfish are a food fish of minor importance in some areas.



1. Ladyfish (*Elops saurus*); 2. Atlantic tarpon (*Megalops atlanticus*). (Illustration by Jacqueline Mahannah)

Species accounts

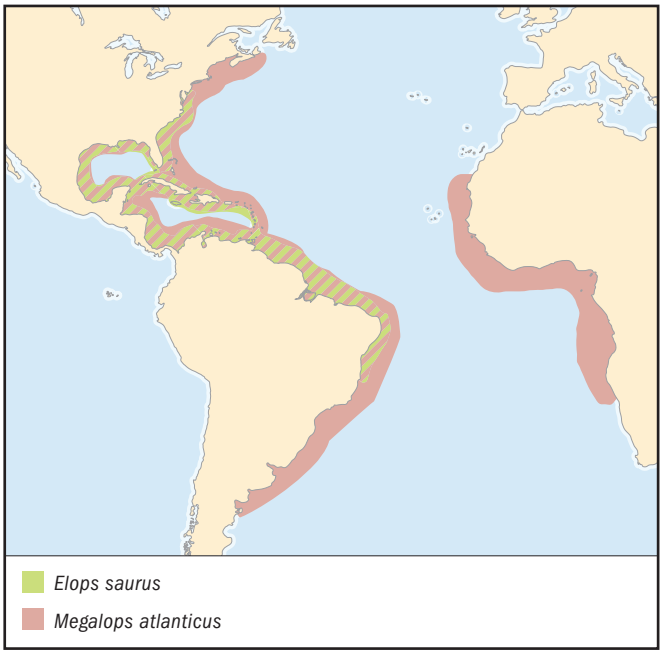
Atlantic tarpon
Megalops atlanticus

TAXONOMY
Megalops atlanticus Valenciennes, 1847, Guadeloupe, Santo Domingo, Martinique, and Puerto Rico.

Anglers have long believed that the tarpon in some areas were different and larger than in other areas, but there is no genetic basis for this belief. While some areas may attract larger fish, these fish are not different genetically from those found elsewhere in the western Atlantic, and they all appear to interbreed freely. However, the tarpon of the eastern Atlantic do appear to be genetically distinct from their western Atlantic cousins. These populations have probably been isolated by the vast expanse of the Atlantic Ocean, and there is little or no interbreeding with western Atlantic tarpon. In is not known if the exceptionally large sizes attained by African tarpon have a genetic or environmental basis, but the isolation of the two stocks indicates that the differences could be genetically based.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Elongate and highly compressed body. Eye large. Mouth oblique with a prominently projecting lower jaw. Large, thick, prominent scales. Teeth small and feel like sandpaper when touched. All fins are soft rayed. A single dorsal fin is located behind the pelvic fins but entirely before the anal fin; the dorsal fin has a distinctive and greatly prolonged final ray. The final ray of the anal fin is also somewhat elongate, but much less so than that of the dorsal fin. Deeply forked caudal fin. Tarpon are bright silvery all over, and the back is darker than the sides or belly.



DISTRIBUTION
Both sides of the tropical and subtropical Atlantic Ocean. In the western Atlantic, tarpon regularly occur from the eastern shore of Virginia to central Brazil and throughout the Caribbean Sea and Gulf of Mexico, as well as off Central and South America. At least seven records exist from as far north as Nova Scotia, where a few large tarpon have been captured between August and October. Tarpon also are present in the eastern Atlantic off the coast of tropical Africa and are occasionally found as far north as Portugal and France. There is a single record of a tarpon from Ireland. African tarpon are known to reach exceptionally large sizes, and many recent world records have come from this area, including some unconfirmed reports of 330.7-lb (150-kg) fish. Tarpon are sexually dimorphic, and females reach much larger sizes than males.

HABITAT
Young-of-the-year tarpon occur in small stagnant pools and sloughs of varying salinity and have been reported from North Carolina, Georgia, Florida, Texas, Caribbean islands, Costa Rica, and Venezuela. In tropical areas, juvenile tarpon typically occur in mangrove habitats, often in water with low dissolved oxygen levels. Tarpon occur in salinities ranging from freshwater to more than 45 parts per thousand and are capable of surviving temperatures of at least 105°F (65.6°C), but they suffer mortalities at temperatures of 50–55°F (10–12.8°C). Large numbers of tarpon die during severe cold fronts off Florida.

BEHAVIOR
Anglers often detect the presence of schools of tarpon by observing individuals "rolling" at the surface. The tarpon's habit of rising to the surface and breathing air is unusual among marine species, although this practice is common among tropical freshwater swamp-dwelling fishes. Breathing air is accomplished by way of a highly vascularized swimbladder that functions as an air-breathing organ. The swimbladder is an elongate, balloon-like sac located above the viscera and just below the backbone. In most fish species, the swimbladder acts as a buoyancy control mechanism. The fish can adjust the volume of air in the bladder and remain neutrally buoyant. In tarpon, this swimbladder is connected to the gut by a duct enabling the tarpon to gulp air and ventilate the swimbladder. Young tarpon, when held in experimental chambers from which all of the dissolved oxygen has been removed, are able to meet their oxygen needs by breathing air. This adaptation allows tarpon to survive in water with low dissolved oxygen concentrations such as commonly encountered by juveniles in hot, stagnant mangrove marshes. Experimental work also suggests that tarpon are facultative air-breathers, and in well-oxygenated waters are able to meet their oxygen requirements without breathing air. Young tarpon can survive in well-oxygenated water when deprived of the opportunity to reach the surface and breathe air. However, after several unsuccessful attempts to reach the surface they have emptied their swimbladders and become negatively buoyant until allowed access to the surface again.

FEEDING ECOLOGY AND DIET
Small tarpon (0.6–3.0 in [16–75 mm]) feed predominantly on cyclopoid copepods, fishes, caridean shrimp, and mosquito larvae. No detailed studies have examined the feeding habits of large tarpon, but anecdotal information suggests that a wide

variety of fishes are consumed, including mullet (*Mugil* spp.), pinfish (*Lagodon rhomboides*), ariid catfishes, and clupeids, as well as crabs and shrimp.

REPRODUCTIVE BIOLOGY

Female tarpon are larger than males regardless of capture location, and average fish size varies geographically. Sexually mature Florida females average about 110 lb (50 kg) and can exceed 220 lb (100 kg). In contrast, sexually mature Florida males average only 66 lb (30 kg), and they rarely exceed 110 lb (50 kg).

Tarpon from Costa Rican waters are year-round spawners, unlike tarpon from other areas. Inactive or resting ovaries are rare in Costa Rica females, suggesting that females spawn repeatedly throughout the year and have no extended period of inactivity. In Florida, tarpon spawning is seasonal and peaks between May and July. By August, most females are finished spawning. In the Southern Hemisphere, off the northeast coast of Brazil, researchers have reported that tarpon spawn from October to January—during the Southern Hemisphere's spring and summer.

Ripe tarpon ovaries are large and can contain up to 20 million maturing oocytes and many more small resting oocytes. "Oocyte" is the proper name of a developing egg that has not ovulated and is not yet ready to be spawned. Although hundreds of mature female tarpon have been examined during the spawning season, none have been caught in the act of spawning. This is probably because spawning occurs in areas not typically fished. Even though the number of eggs released by a female in a single spawning event is unknown, the numbers of developing oocytes in the ovary suggests that their reproductive output is immense.

Tarpon are relatively long lived and can live more than 50 years. By age one, tarpon are about 1.5 ft (450 mm) long and are common in rivers and the upper reaches of estuaries, where they remain until reaching sexual maturity. In Florida, sexual maturity is reached at an age of about 10 years. After attaining sexual maturity, tarpon become more coastal in habitat and are most numerous around inlets and off beaches. Large tarpon targeted by anglers in Florida are typically from 15 to 35 years old.

CONSERVATION STATUS

Florida's fishery is intensely regulated, and anglers must purchase a $50 permit before harvesting a fish. Since the establishment of the permit system in 1989, the harvest of tarpon in Florida has declined to fewer than 100 fish per year, and the fishery is now mostly catch-and-release. Encouraging catch-and-release fishing for tarpon has been an effective management strategy, because the vast majority of released fish survive to be caught again. The sale of tarpon in Florida is prohibited, but in most of their range tarpon have never been considered a desirable food fish.

SIGNIFICANCE TO HUMANS

In Central America and South Florida, tarpon are the basis of economically important recreational fisheries. Tarpon occur in a variety of habitats ranging from freshwater lakes and rivers to offshore marine waters, but large tarpon targeted by Florida's fishery are most abundant in estuarine and coastal waters. In Florida, the fishery is seasonal; most tarpon are caught between May and July, although some fish are caught in all months. Tarpon are known for their spectacular leaps from the water when hooked and for their willingness to enter shallow water and eat artificial baits. Probably more than any other species, tarpon offer anglers in small boats an opportunity to pursue a large gamefish. Tarpon are pursued by a large for-hire charter boat fleet in Florida. ◆

Ladyfish

Elops saurus

TAXONOMY

Elops saurus Linnaeus, 1766, "Carolina." The taxonomic status of *Elops saurus* is unclear, and this name may be applied to more than one species.

OTHER COMMON NAMES

None known.

DISTRIBUTION

Abundant from North Carolina south through the Gulf of Mexico and into the Caribbean.

PHYSICAL CHARACTERISTICS

Ladyfish have a single, soft-rayed dorsal fin that originates about midway along the back. The pelvic fins are located midway between the tip of the snout and the fork of the deeply forked caudal fin. Scales are small and thin. Ladyfish are silvery all over; the back is bluish, and the lower parts of the sides and the belly are yellowish.

HABITAT

Common in estuaries and coastal waters of tropical and subtropical latitudes. Often occur in large schools. Tolerant of a wide range of salinities but seldom occur in freshwater.

BEHAVIOR

Little is known other than general descriptions of feeding habits and reproductive migrations. Ladyfish can be extremely abundant and most often occur in large schools. They are voracious predators.

FEEDING ECOLOGY AND DIET

Ladyfish feed principally in midwater on pelagic prey. Feeding is mainly on fish, but decapod crustaceans also are consumed.

REPRODUCTIVE BIOLOGY

Spawning appears to occur offshore. Larvae are common in the Gulf of Mexico and off the southern United States, where they have been reported as far north as Virginia. Fertilized eggs are undescribed. Spawning may occur throughout the year but probably peaks during fall in Florida and in the Gulf of Mexico.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Ladyfish are often caught by recreational anglers but are seldom a targeted species. Ladyfish are voracious predators and will attack a variety of lures and baits. The species is fished commercially in Florida and sold both for human consumption and as bait to recreational anglers.

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Roy Eugene Crabtree, PhD

Albuliformes
(Bonefishes and relatives)

Class Actinopterygii
Order Albuliformes
Number of families 3

Photo: Bonefishes (*Albula vulpes*) are found in most of the warm seas of the world. (Photo by Tom McHugh/Shedd Aquarium/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Albuliformes includes three extant families: Albulidae, Notacanthidae, and Halosauridae. The bonefish family (Albulidae) contains two genera: *Albula*, with possibly eight species, and *Istieus*, with two species. The halosaur family (Halosauridae) contains three genera: *Aldrovandia*, with six species; *Halosaurus*, with nine species; and *Halosauropsis*, with one species. The marine spiny eel family (Notacanthidae) contains three genera: *Lipogenys*, with one species; *Notacanthus*, with six species; and *Polyacanthonotus*, with four species. The fossil record for this order extends back almost 100 million years.

Physical characteristics

In Albulidae (bonefishes) the body is moderately slender. The snout is distinctively pointed and conical. The mouth is inferior, and the snout projects well beyond the tip of the lower jaw. All fins lack spines. The dorsal fin originates at about the midpoint of the body in *Albula*. In *Istieus* the dorsal fin origin is more forward, and the fin is elongate, extending nearly to the caudal fin. The anal fin is short and originates well behind the base of the dorsal fin. The pelvic fins are positioned below the last dorsal fin rays in *Albula* and under the middle of the dorsal fin in *Istieus*. Scales are small. Most fishes are less than 3.3 ft (1 m) in length. The back of *Albula* is blue-green in color, with narrow, dark horizontal lines that fade rapidly after death. The sides are silvery.

Halosaurs have an elongate, eel-like body, which tapers to a point. There is no caudal fin. The anal fin is elongate and extends along the posterior half of the body. There is a single short dorsal fin located just before the midpoint of the body. All fins have soft rays with no spines. The mouth is inferior, and the snout projects well beyond the tip of the lower jaw. Most fishes are less than 3.3 ft (1 m) in length. Colors range from tan to black.

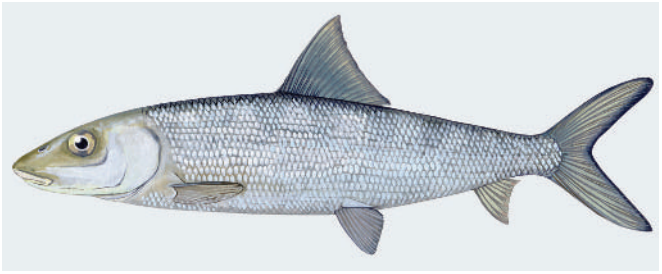
The Notacanthidae, or marine spiny eels, have an elongate, eel-like body, which tapers to a point with little or no caudal fin. The anal fin is elongate and extends along the posterior half of the body. The anal fin consists of spines anteriorly grading to soft rays posteriorly. The dorsal fin in most species has from 26 to 41 isolated spines, from which the family's common name "spiny eels" derives. The mouth is inferior, and the snout projects beyond the tip of the lower jaw. Most fishes are less than 3.3 ft (1 m) in length. The coloring is typically tan.

Distribution

This order is worldwide in distribution. The family Albulidae occurs in shallow tropical waters worldwide. The Notacanthidae and Halosauridae are little-known families of deep-sea fishes that occur along the continental slope and rise of the world's oceans at depths from 3,281 to 9,843 ft (1,000–3,000 m). Bonefish (*Albula*) frequent coastal and inshore waters of tropical seas worldwide. In the western Atlantic, bonefish regularly occur in the Florida Keys and the Bahamas and throughout the Caribbean. Halosaurs and spiny eels are deep-sea fishes of worldwide distribution.

Habitat

Bonefish are common in tropical shallow-water areas. They are most abundant at depths of less than 115 ft (35 m) and often feed in water less than 3.3 ft (1 m) deep. Bonefish can be found over shallow grass flats and in sandy areas. Juvenile bonefish and metamorphic larvae occur along sandy beaches with scattered patches of sea grass in water from 1



Bonefish (*Albula vulpes*). (Illustration by Emily Damstra)

to 4.3 ft (0.3–1.3 m) deep. In southern Florida bonefish larvae recruit to sandy beaches during winter and early spring and are found in water temperatures ranging from 60.8 to 82.8°F (16.0–28.2°C) and salinity levels ranging from 10.4 to 37.0 ppt.

Halosaurs typically are found at depths of 1,640–13,123 ft (500–4,000 m) on the continental slope and rise. Spiny eels usually are found at depths of 656–11,483 ft (200–3,500 m) on the continental slope and rise. They generally hover just above the bottom.

Behavior

Bonefish are remarkable because of their common presence in extremely shallow water (less than 1.6 ft, or 0.5 m). The fisheries for bonefish in most areas require specialized boats capable of entering shallow water with little or no noise. Fish typically swim in small schools of five to 20 individuals, although larger schools of more than 100 individuals are not uncommon. Anglers searching for bonefish often detect their presence by spotting their tails protruding from the water as the fish dig in the bottom to feed.

Feeding ecology and diet

Bonefish feed on a variety of small benthic and epibenthic invertebrates and fishes. Feeding often takes place in shallow water, where foraging bonefish are seen with their fins protruding from the water. As they forage, bonefish schools frequently dig in the bottom and disturb considerable quantities of mud and sand. Xanthid crabs, toadfish (*Opsanus beta*), portunid crabs, alpheid shrimp, and penaeid shrimp make up most of the diet of populations in southern Florida. In some areas mollusks and small worms are important in the diet. Juvenile bonefish feed on a variety of polychate worms and small crustaceans, principally copepods, amphipods, and caridean shrimp. Bonefish are subject to occasional predation by sharks.

Halosaurs feed primarily on benthic prey, including worms and small benthic and epibenthic mollusks and such crustaceans as decapods and amphipods. Larger species also consume various fish. Spiny eels feed mainly on small benthic macrofauna, including worms and small crustaceans, such as amphipods and mysids. Species of the genus *Notacanthus* have specialized teeth that form a continuous serrated cutting edge probably used to crop sessile invertebrates. Little is known about which animals prey on halosaurs or spiny eels.

Reproductive biology

In Florida male bonefish reach sexual maturity at a fork length (measured from the tip of the snout to the fork in the tail) of about 15.7 in (400 mm) and an age of about 3.5 years. Florida females reach sexual maturity at a somewhat larger size, about 19.7 in (500 mm), and an age of about four. Gonadal activity is seasonal and peaks from November to May. Yolked oocytes are present in the ovaries in every month except August and September and are most abundant November to May. In Florida juvenile bonefish and post larvae recruit to sandy beach areas during winter and spring. Total fecundity ranges from 0.4 million to 1.7 million oocytes and increases with fish weight. Spawning areas of bonefish are unknown. Larvae reach a maximum size of about 3 in (76 mm). Bonefish live for at least 19 years. Growth of the bonefish is rapid until the age of about six years and then slows considerably.

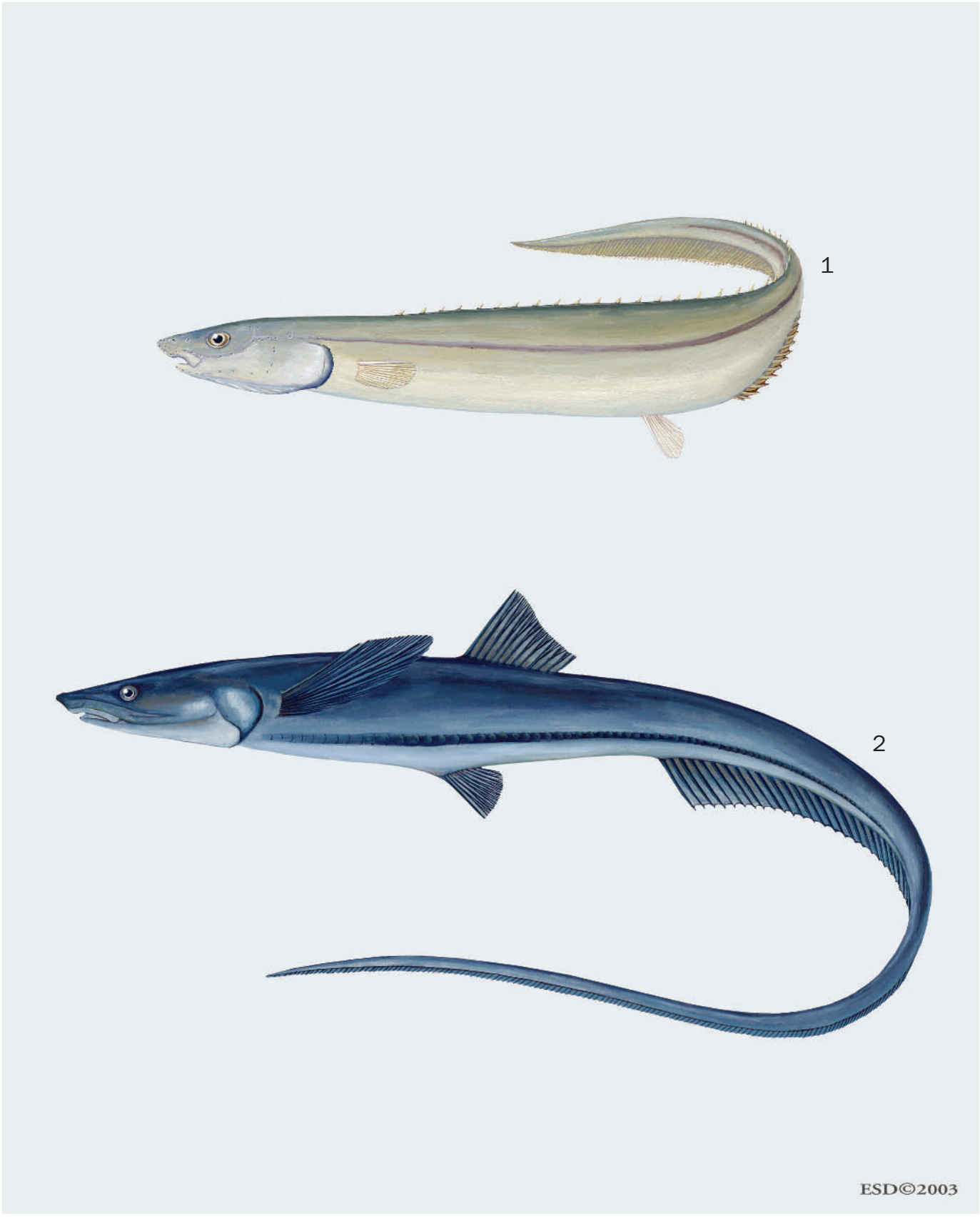
Little is known about halosaur or spiny eel reproduction. In halosaurs spawning appears to be seasonal in some species, but others spawn year-round. It is unknown where the eggs and larvae develop. In spiny eels spawning occurs year-round. It is unknown where the eggs and larvae develop. Spiny eels have remarkable leptocephalus larvae that can reach lengths of 3.3–6.6 ft (1–2 m). Aside from their extremely large size, the larvae resemble those of eels in appearance.

Conservation status

No species of Albuliformes are included on the IUCN Red List.

Significance to humans

In many areas of the species' range, including the waters off the Florida Keys, bonefish are the basis of economically important recreational fisheries, among them a for-hire charter boat fishery in the Florida Keys. Bonefish are renowned by anglers for their wariness and fighting abilities and often are caught in water as shallow as 1 ft (0.3 m). In the Florida Keys fishing for bonefish is a year-round activity and provides a significant source of income to professional fishing guides. The commercial sale of bonefish in Florida is prohibited; the limits placed upon the recreational fishery for bonefish are a bag limit of one fish per angler per day and a minimum fish size of 18 in (457 mm) in total length. Bonefish are not considered a food fish in Florida, and most bonefish are released when caught. Halosaurs and spiny eels are of no commercial value.



1. Marine spiny eel (*Polyacanthonotus merretti*); 2. Halosaur (*Halosauropsis macrochir*). (Illustration by Emily Damstra)

Species accounts

Halosaur
Halosauropsis macrochir

FAMILY
Halosauridae

TAXONOMY
Halosaurus macrochir Gunther, 1878, off Gibraltar.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Elongate, eel-like body, which tapers to a point with no caudal fin. The anal fin is elongate and extends along the posterior half of the body. There is a single short dorsal fin located just before the midpoint of the body. All fins have soft rays with no spines. The mouth is inferior, and the snout projects well beyond the tip of the lower jaw. Among the largest of halosaurs, reaching a length of almost 3.3 ft (1 m). Can be distinguished from other halosaurs by the deeply pigmented sheath of the conspicuous lateral line. Black in color. Occurs at depths of 3,281–9,843 ft (1,000–3,000 m) in the Atlantic and Indian Oceans. Also reported from waters off New Zealand.

DISTRIBUTION
Eastern Atlantic from Ireland to Mauritania and South Africa; western Atlantic, including Canada to 25°N, and off southern Brazil; western Pacific, including Australia, New Zealand, and Japan; and western Indian Ocean.

HABITAT
Found over the continental slope and rise. Little is known regarding specific habitat requirements. Appears to be widespread.

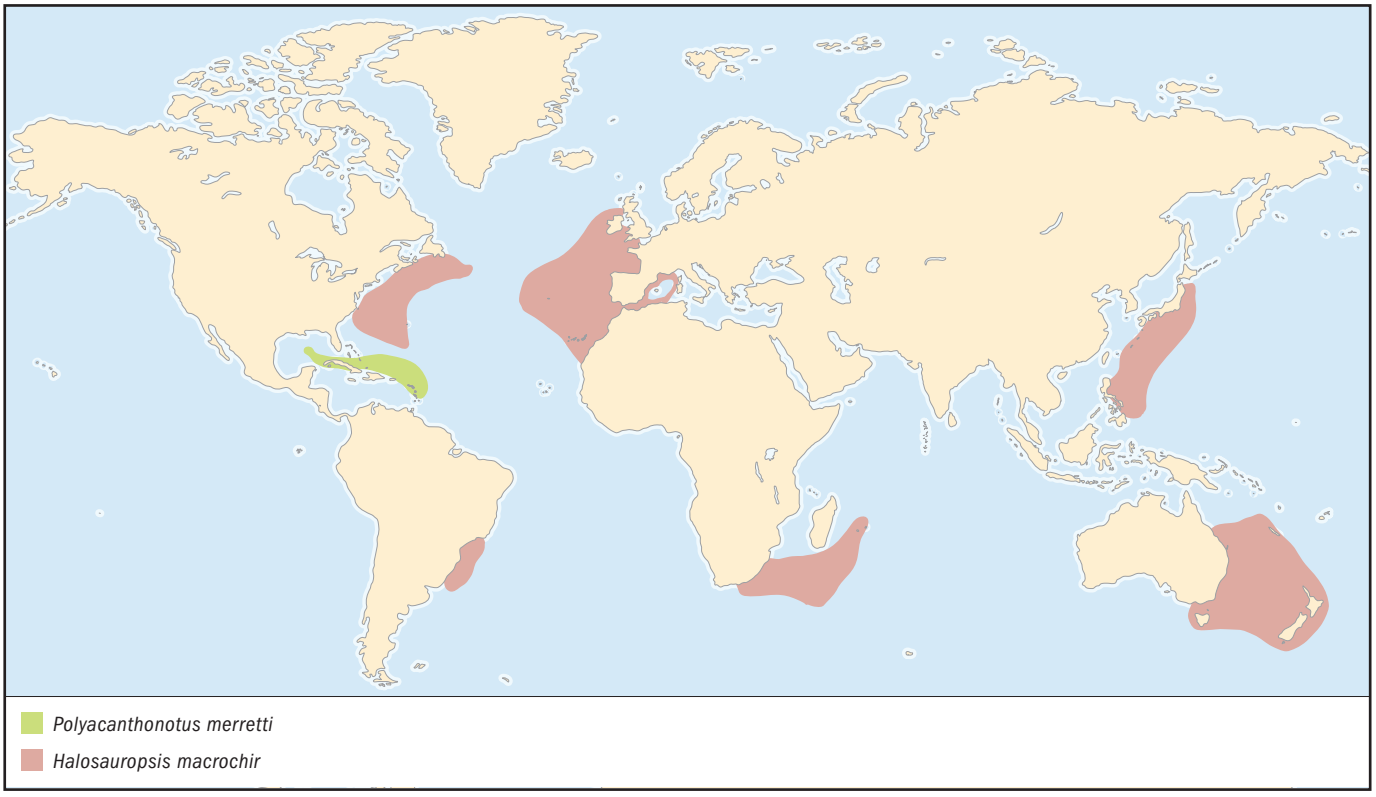
BEHAVIOR
Little is known. Usually seen moving slowly just over the bottom.

FEEDING ECOLOGY AND DIET
Feeds principally on benthic prey, including worms and small benthic and epibenthic mollusks and crustaceans, such as decapods and amphipods. Larger specimens also consume some fish.

REPRODUCTIVE BIOLOGY
Little is known regarding spawning. It is unknown where the eggs and larvae develop. Eggs develop into leptocephalus larvae.

CONSERVATION STATUS
Not listed by IUCN. Stocks probably have not been affected by human activities.

SIGNIFICANCE TO HUMANS
Because of its occurrence at great depths, the species is of no economic importance. ◆



Marine spiny eel

Polyacanthonotus merretti

FAMILY
Notacanthidae

TAXONOMY
Polyacanthonotus merretti Sulak et al., 1984, the Bahamas.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Elongate, eel-like body, which tapers to a point with little or no caudal fin. The anal fin is elongate and extends along the posterior half of the body. It consists of spines anteriorly grading to soft rays posteriorly. The dorsal fin in most species has 28–36 isolated spines. The mouth is inferior, and the snout projects beyond the tip of the lower jaw. Attains a length of about 11.8 in (300 mm). Typically tan in color. Found on both sides of the North Atlantic, predominantly tropical in range. Occurs at depths from 1,969 to 6,562 ft (600–2,000 m); most at 3,281–4,921 ft (1,000–1,500 m).

DISTRIBUTION
Western Atlantic off the Bahamas.

HABITAT
Found over the continental slope and rise. Little is known regarding specific habitat requirements. Appears to be widespread.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Feeds principally on small benthic macrofauna, including worms and small crustaceans, such as amphipods and mysids.

REPRODUCTIVE BIOLOGY
Appears to spawn year-round. It is not known where the eggs and larvae develop. Eggs develop into leptocephalus larvae.

CONSERVATION STATUS
Not listed by IUCN. Stocks probably have not been affected by human activities.

SIGNIFICANCE TO HUMANS
Because of its occurrence at great depths, the species is of no economic importance.

Resources

Books

Hildebrand, S. F. "Family Albulidae." In *Fishes of the Western North Atlantic*, edited by H. B. Bigelow. Vol. 3. New Haven: Sears Foundation for Marine Research, Yale University, 1963.

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Roy E. Crabtree, PhD

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Anguilliformes
(Eels and morays)

Class Actinopterygii
Order Anguilliformes
Number of families 15

Photo: The pale blue, mottled head of an American conger (*Conger oceanicus*) on a rock off the Island of Mahe, in the Seychelles. (Photo by Lawson Wood/Corbis. Reproduced by permission.)

Evolution and systematics

Fossil Anguilliformes are known from the Upper Cretaceous (about 93 million years ago) until the Pliocene (about two million years ago) and have been found in Africa, Europe, North America, the East Indies, Australia, and New Zealand. The Anguilliformes also are called Apodes ("limbless"), because of their lack of protruding fins, and true eels, because there are many other fishes (about 45 families) that do not belong to this group but have similar burrowing habits, and an eel-like shape as a result of convergent evolution. Anguilliformes are related to the Elopiformes (tarpons), the Albuliformes (spiny eels and halosaurs), and the Saccopharyngiformes (snipe and gulper eels) because they all have a leptocephalus, or ribbonlike, larval stage during development. The larval stage groups them into the subdivision or superorder called Elopomorpha. Some researchers, such as Filleul and Lavoué, have questioned this phylogenetic relationship based on molecular studies. Nelson divided this order into three suborders and 15 families (Anguillidae: 15 spp.; Heterenchelyidae: 8 spp.; Moringuidae: 6 spp.; Chlopsidae: 16 spp.; Myrocongridae: 2 spp.; Muraenidae: 200 spp.; Synaphobranchidae: 26 spp.; Ophichthidae: 250 spp.; Colocongridae: 5 spp.; Derichthydae: 3 spp.; Muraenesocidae: 8 spp.; Nemichthydae: 15 spp.; Congridae: 150 spp.; Nettastomatidae: 30 spp.; Serrivomeridae: 10 spp.). Much more work is needed in this area to determine the exact phylogenetic relationships within this group.

Physical characteristics

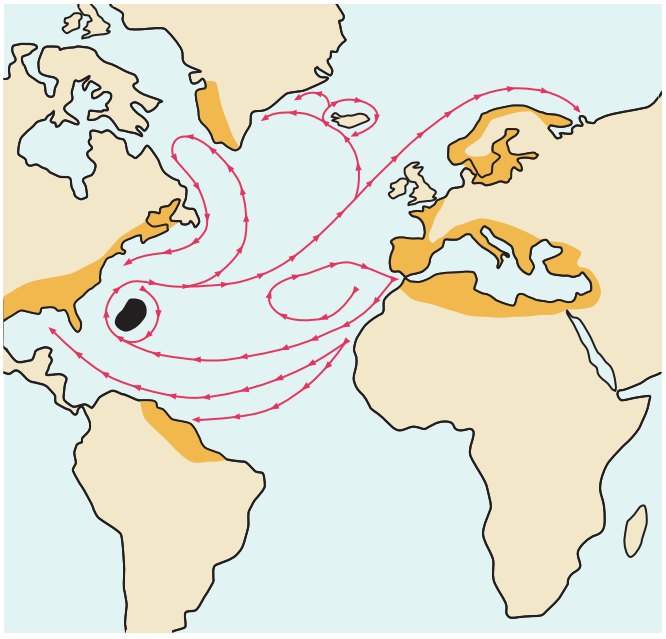
In addition to their eel-like bodies, anguilliform species have widely varying coloration that ranges from black or dark gray in deep-sea species to rich colors and complex patterns in tropical reef species. Adult sizes range from about 4 in (10 cm) to 11.5 ft (3.5 m), as in the moray species *Thyrsoidea macrura*. Systematists have emphasized numerous other morphological characteristics that have been found useful for phylogenetic purposes, including the lack of pelvic fins and the continuous dorsal, anal, and caudal fins that can have up to 650 soft rays, giving some individuals the appearance of having a pointed tail. Most species do not have pectoral fins, but when they are present, they lack bony connections to the skull. Most species also lack scales; in those species that have them, they are cycloid in type and embedded under the skin. The gill openings usually are narrow, with the gill region elongated and the gills displaced posteriorly. These species also have lost gill rakers. The skeleton is reduced, but the vertebrae may number as many as 700. They lack both pyloric caeca and oviducts but have retained the swim bladder. In summary, this order has many morphological simplifications or losses as a result of their evolutionary trend toward a wormlike configuration; the increased number of vertebrae is the result of the same phenomenon.

Distribution

Both the current distribution and the fossil record indicate that the members of this order always have occupied the same geographical areas, that is, tropical and temperate ocean. Anguilliformes are found in rivers draining into the North Atlantic, Baltic, and Mediterranean. They also have been introduced into Asia, South America, and Central America, but for the most part they have not reproduced in those areas. However, Anguillidae have a more restricted distribution, and do not inhabit the eastern Pacific and South Atlantic.

Habitat

The order Anguilliformes can be found in a wide variety of marine, brackish, and freshwater habitats, including streams,



Migration pattern of the American eel and the European eel. (Illustration by Barbara Duperron)

lakes, deep-sea waters, and coral reefs. Some representatives of this order are catadromous, meaning that adults spend most of their lives in estuaries and freshwater and then move to the sea to spawn. The same species can be found in marine, estuarine, and freshwater environments. While some are pelagic, most are found living in small openings in coral reefs and rocks or burrowing in soft substrates. In general, morays and congers inhabit coral reefs and rock crevices, whereas certain congrids of the subfamily Heterocongrinae form vast colonies of up to several hundred individuals in tropical reef areas. Despite the fact that they favor these specific habitats as adults, all of the leptocephalus larvae form part of the marine plankton at one time or another in their life cycle.

Behavior

One of the most extraordinary aspects of their biology is their ability to migrate, yet they are slow swimmers. They swim by means of sinuous lateral movements of the body and median fins. Another interesting aspect of their swimming behavior is the ability of burrowing species to swim backward, which allows them to retreat rapidly into their burrows while still being able to look at any potential enemy. Although they can congregate in large numbers under specific circumstances, both larvae and adults do not form schools and thus can be considered to be solitary.

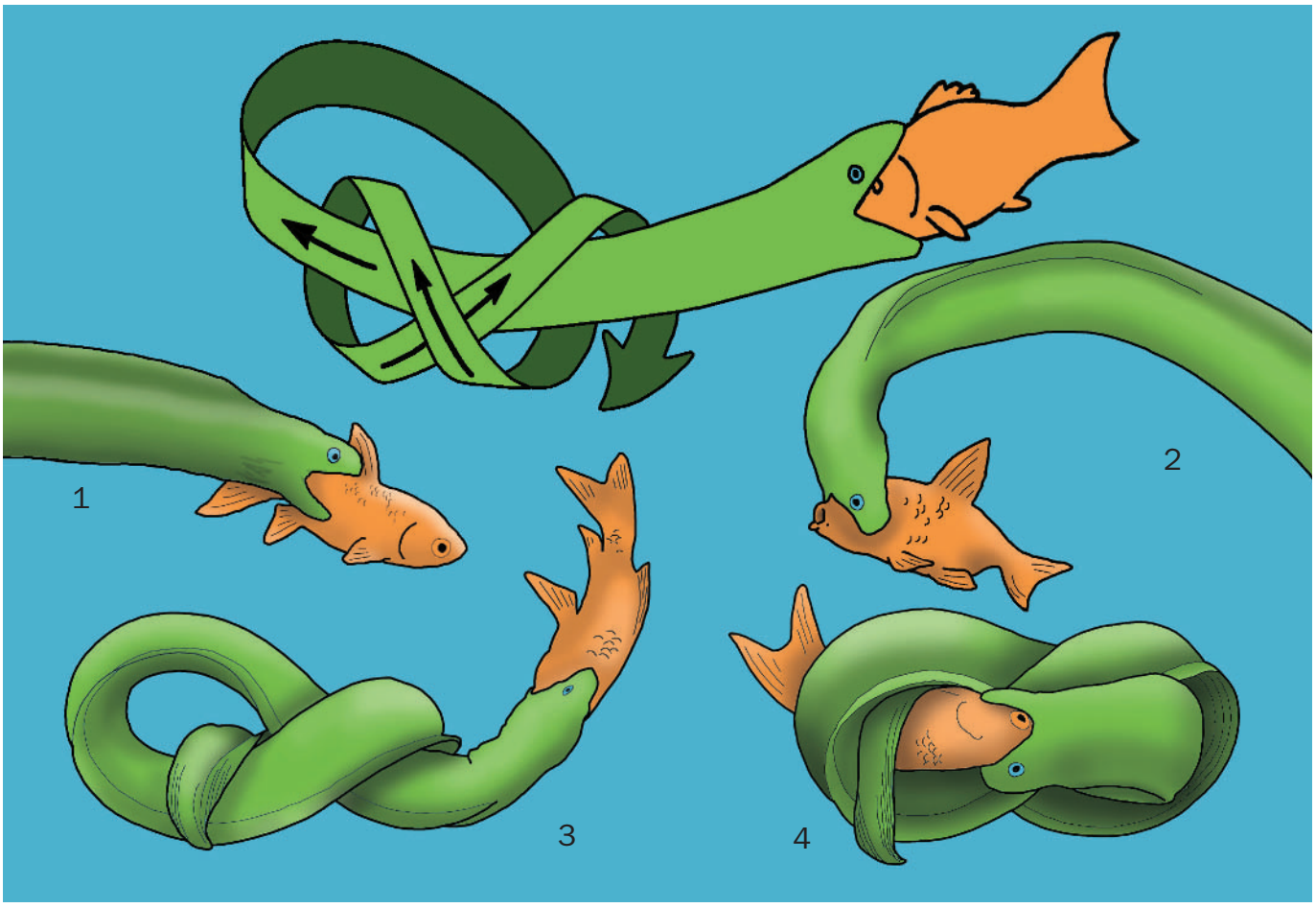
Feeding ecology and diet

The species of this order can be labeled generalists and opportunistic feeders, to the point that virtually any animal species they encounter can become a source of food for them, from aquatic insects in freshwater to crustaceans and many other species of fishes. This flexibility toward food items and even feeding habits is evident during development: depending upon the stage of development, they will shift toward the most appropriate food source and capturing tactics. Extreme cases include the parastic snubnosed eel, *Simenchelys parasitica*, which burrows into the tissues of other species of fish. They can attach themselves to the heart of their host, from which they consume the blood. Other species feed on dead animals that lie on the bottom, including whales. This has led to a renewed interest in the ecological role played by some anguilliforms in benthic habitats, including the recycling of nutrients. Anguilliformes are preyed upon mostly by other types of fish. When they are in larval form, small fish and even some invertebrates will prey on them. As they grow larger, the size of their predators also increases.

Reproductive biology

The migratory and reproductive biological characteristics of anguilliforms are intertwined closely; thus, one cannot be explained without explaining the other. Although the life cycle of every anguilliform species has yet to be studied, it is believed that all of them undergo the same complex path of development, regardless of the final habitat they occupy. Fertilization among these fishes is external, and the eggs are relatively large (about 0.98 in, or 2.5 mm), which allows them to undergo extended development even before being able to

A yellow moray (*Gymnothorax prasinus*) in Wreck Bay, New South Wales, Australia. (Photo by Animals Animals ©A. Kuiter-OSF. Reproduced by permission.)



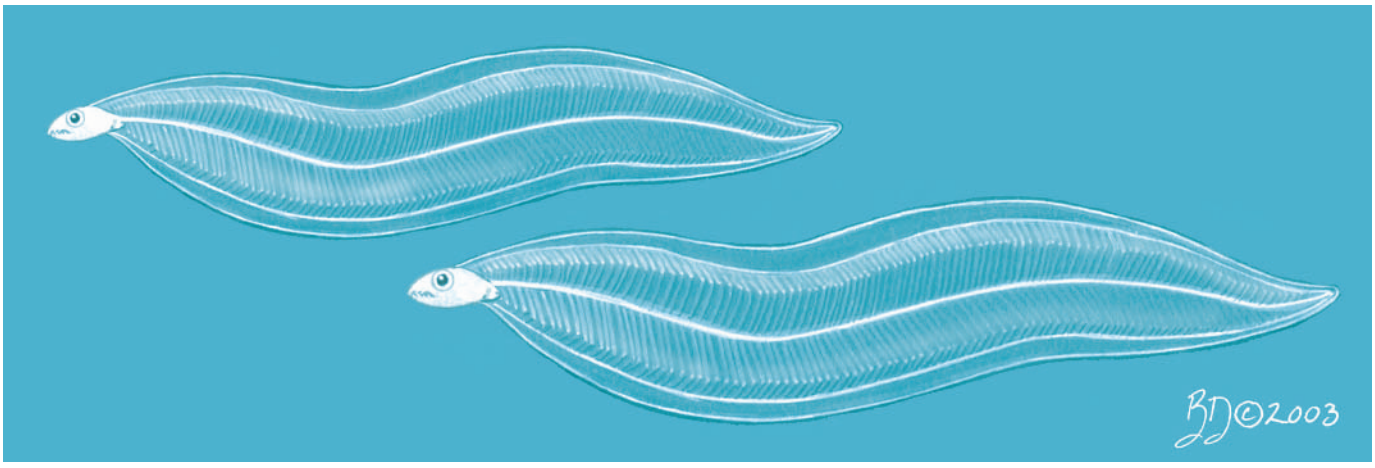
Certain eels possess the ability to tear apart prey items by tying themselves into a knot in order to obtain leverage against the prey item. The general procedure is this: (1) the eel grabs a fish that is too large to swallow whole, often by the head (2). The tail of the eel then turns back toward the eel's body and forms a series of interlacing loops which forms a knot similar to a square knot or a figure-eight knot (3). This knotting process continues until the heads of the eel and prey contact the knotted eel's body. The eel then pulls its own head through the knot and with it a mouthful of food (4). The prey fish is generally decapitated by this action. The eel then bites onto another section of the prey animal and the process continues. (Illustration by Dan Erickson)

feed. The eggs hatch, producing a prolarva, which in turn transforms into the leptocephalus larva.

The leptocephalus larva is so singular that biologists have studied it closely since the nineteenth century, when many researchers thought these larvae were actually adult fishes, given their complex morphologic features and behavior. They are elongated and laterally compressed while being transparent and gelatinous, which could make them difficult to detect. Although there is a great deal of morphological diversity among leptocephalus larvae, they all have a small and round caudal fin that is continuous with the dorsal and anal fins. This gives them varied shapes that are leaflike in appearance. In fact, the diversity of larval morphological features even within the same species is such that it is difficult to tell which larva belongs to which adult form. A couple of important characteristics of these larvae is their W-shaped myomeres (muscle packages) and prominent sharp teeth. These two features, together with their size, usually 2–4 in (5–10 cm) in length, make them sustained swimmers and powerful predators of other planktonic organisms. Some, like the slender snipe eel, *Nemichthys scolopaceus*, can reach 18 in (45 cm) in length, undoubtedly very large for fish larva.

Leptocephalus larvae can be found at varying depths, from the surface of the ocean to 1,600 ft (500 m). As opportunistic feeders, they eat anything that is available, from diatoms to small crustaceans and other fish larvae. By the same token, they are preyed upon by different species of fish. It has been calculated that, on average, of six million eggs released by the European eel, *Anguilla anguilla*, only one survives to reach adulthood.

Leptocephalus larvae undergo metamorphosis in the open ocean after a period that ranges from six months to three years. In general, it can be said that the colder the waters, the longer the larval stage. The juveniles usually look like smaller versions of the adults. These juveniles are the product of many changes that can be summarized as follows: (a) reduction in the total body mass (up to 90% of weight) and body length, making the initial juvenile smaller than the larva itself; (b) transformation of the leaflike shape into a cylindrical shape;



Eels go through a larval (leptocephalus) stage during which they are paper-thin, as shown by these American eel larvae (*Anguilla rostrata*). (Illustration by Barbara Duperron)

(c) loss of larval teeth; (d) loss of larval melanophores (pigment cells); (e) loss of pectoral fins; and (f) change in the position of the dorsal fin to much farther back.

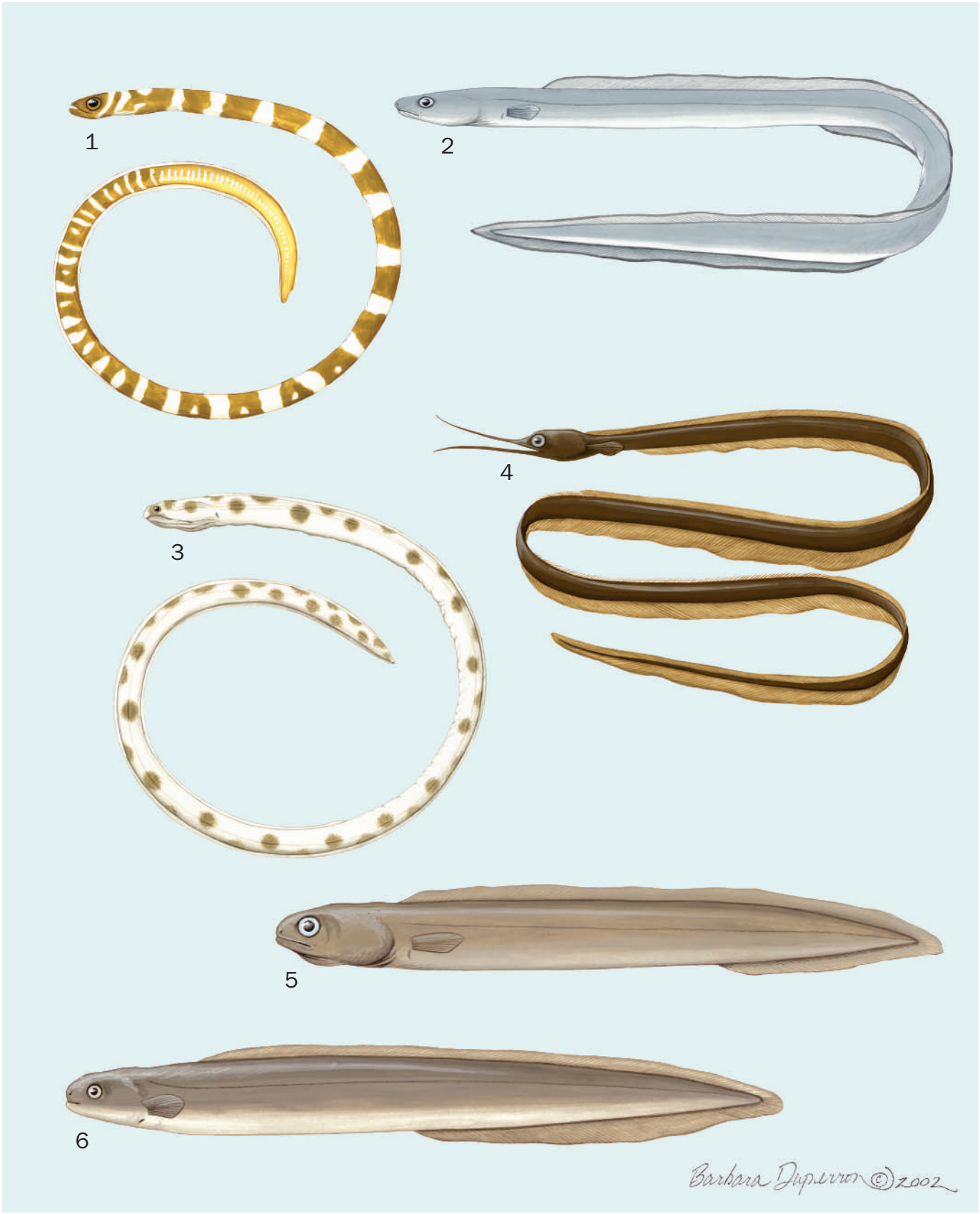
The juveniles use oceanic currents to disperse; once they have occupied what is going to be their habitat as adults, they continue to grow and mature. This process can be quite lengthy, up to 10 years for some species. The complexity of this process also involves their sexual maturation, which includes phases of neutrality, precocious feminization, and juvenile hermaphroditism before they become adult males or females. As in some reptiles and other species of vertebrates, the sex ratio (proportion of males to females) can be the result of environmental factors (the more stressful the environmental conditions, the higher the proportion of females). Once true eels become fully adult, they undergo either a short-distance or a long-distance migration to a spawning area.

Conservation status

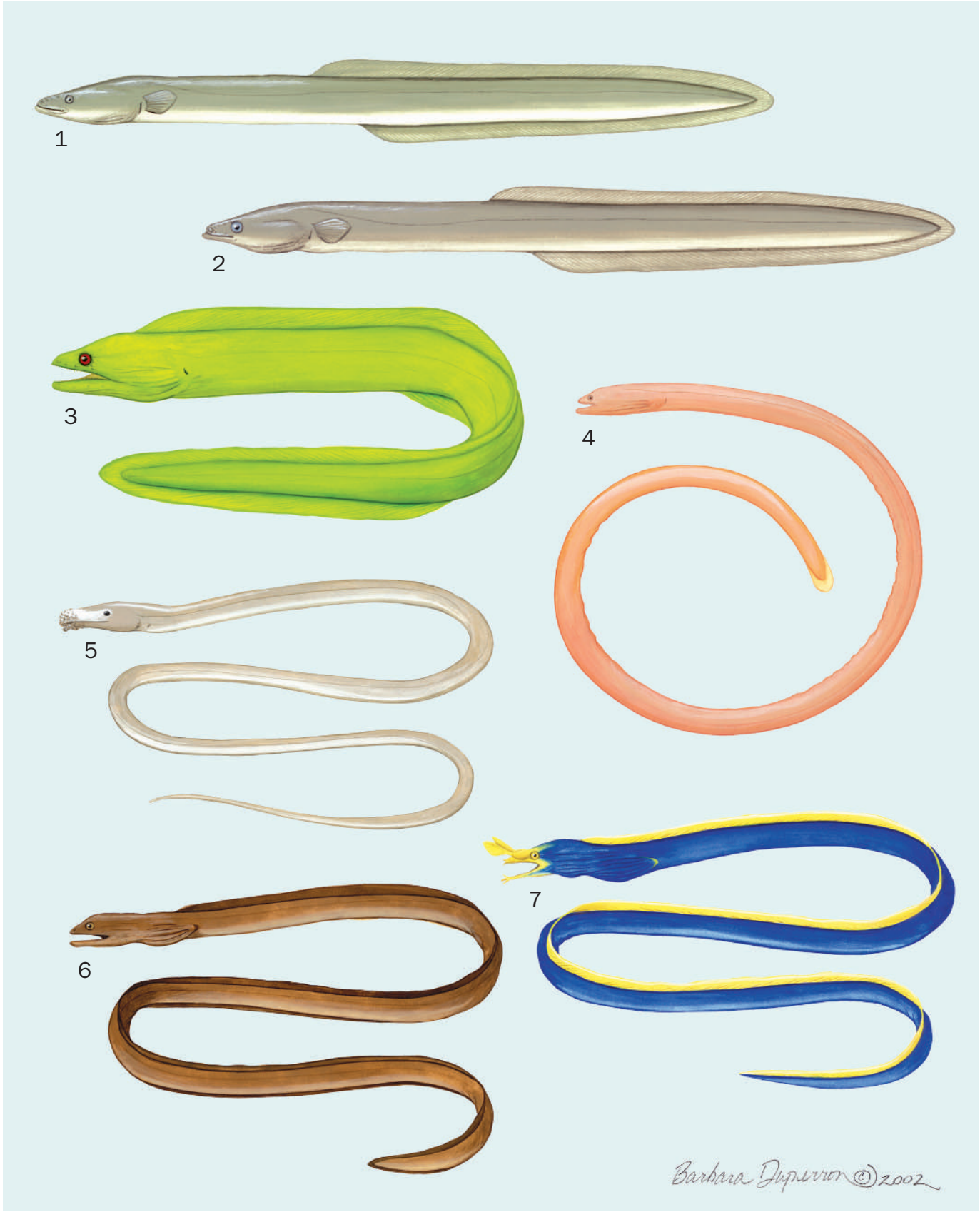
No anguilliform species have been listed by the IUCN under any category. With freshwater habitat modification and the threat posed to coral reefs all over the world, however, several species could be considered threatened in one way or another.

Significance to humans

Eels, whether "true eels" or otherwise, have been mentioned in mythology from ancient Greece to Polynesia. Today, only the freshwater eels (family Anguillidae) are of major economic importance in areas in which they are abundant, because of their value as food at both juvenile and adult stages. Some morays and congers are popular in public aquaria and among marine aquarists.



1. Splendid garden eel (*Gorgasia preclara*); 2. American conger (*Conger oceanicus*); 3. Tiger snake eel (*Myrichthys maculosus*); 4. Slender snipe eel (*Nemichthys scolopaceus*); 5. Froghead eel (*Coloconger raniceps*); 6. Snubnosed eel (*Simenchelys parasitica*). (Illustration by Barbara Duperron)



1. European eel (*Anguilla anguilla*); 2. American eel (*Anguilla rostrata*); 3. Green moray (*Gymnothorax funebris*); 4. Rusty spaghetti eel (*Moringua ferruginea*); 5. Pignosed arrowtooth eel (*Dysomma brevirostre*); 6. Slender giant moray (*Strophidon sathete*); 7. Ribbon moray (*Rhinomuraena quaesita*). (Illustration by Barbara Duperron)

Species accounts

European eel
Anguilla anguilla

FAMILY
Anguillidae

TAXONOMY
Muraena anguilla Linnaeus, 1758, "Europe." Tucker (1959) suggested that the European eel and the American eel, *A. rostrata*, are the same species.

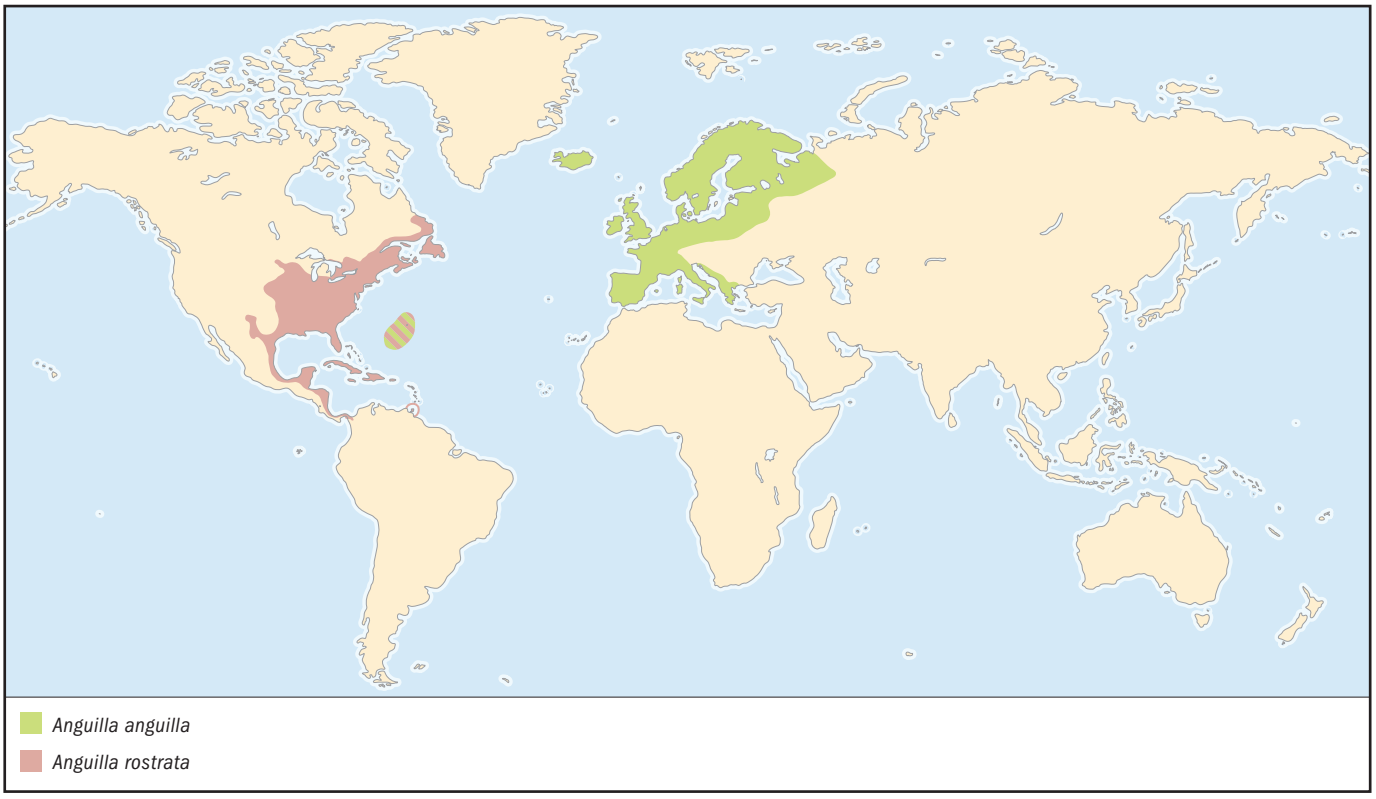
OTHER COMMON NAMES
English: Common eel; French: Anguille; German: Aal; Spanish: Anguila.

PHYSICAL CHARACTERISTICS
Specimens have been reported to reach 52.36 in (133 cm) in length, with a weight of 14.548 lb (6.599 kg). Distinguished from other types of freshwater eels mostly by the number of vertebrae, which range from 110 to 119. Color greenish-brown to yellowish-brown. It has small vertical gill openings that are restricted to the sides. The lower jaw is slightly longer and projects. The dorsal fin originates far behind the pectoral fins, whereas the anal fin originates slightly behind the anus and well back from the origin of the dorsal fin.

DISTRIBUTION
Rivers of the North Atlantic, Baltic, and Mediterranean, along the coasts of Europe from the Black Sea to the White Sea. Its spawning area is the western Atlantic, specifically the Sargasso Sea. It has been introduced successfully into Finland and Romania. Introductions in Norway, Israel, Japan, Taiwan, Brazil, Indonesia, California, Eritrea, and Jordan have not been successful.

HABITAT
Waters where the temperatures range from 32–86°F (0–30°C). Young eels grow in freshwater where they stay for 6–12 years (males) or 9–20 years (females). After becoming sexually mature, they migrate to the sea, where they can be found in deep waters living on the bottom, under stones, in the mud, or in crevices. Spawning takes place in the Sargasso Sea. The larvae are brought by the Gulf Stream to the coasts of Europe. They evolve into small eels before moving into freshwater basins.

BEHAVIOR
The European eel spawns in the Sargasso Sea in the subtropical northwestern Atlantic Ocean. Their larvae, leptocephali, are transported by the Gulf Stream and North Atlantic current system to Europe. Despite being an individualistic species, large groups of elvers and young eels can be observed from time to time in estuaries and rivers. An elver is a small cylindrical young eel, more advanced in development than a leptocephalus larva but less developed than an adult eel. Those congregations of elvers and juveniles are not fish schools in the real sense of the word (active assembling for selective advantages such as protection against predators or reproduction) but rather a mass response to environmental conditions. When elvers and young eels are observed in mass from time to



time in estuaries and rivers, it is because they are responding individually to particular ecological conditions and not because they are actually forming schools.

FEEDING ECOLOGY AND DIET
Opportunistic feeders. They include among their food items almost any species of aquatic fauna, freshwater as well as marine, that they encounter. Adults do not feed during migration to sea. Other eels, herons, cormorants, pikes, and gulls prey upon them.

REPRODUCTIVE BIOLOGY
The American eel (*A. rostrata*) and the European eel (*A. anguilla*) spawn in Sargasso Sea, located in the subtropical northwestern Atlantic Ocean, between January and May. Their larvae, leptocephali, are transported by the Gulf Stream and North Atlantic current system to North America and Europe, respectively.

Before entering the continental coastal zones and estuaries, the leptocephali transform into elvers. Once there, and before entering the freshwaters, they develop into small (juvenile) eels. The young eels spend their growing period in freshwater, where males stay for 6 to 12 years; females spend from 9 to 20 years there. While in freshwater, they live on the bottom under stones or in the mud or rock crevices. At the end of their growth period, the eels become sexually mature and migrate to the sea, where they inhabit deep waters.

There is a significant differential in time in the life cycle span between both species. The overall mean age of European elvers is 350 days at metamorphosis (from leptocephalus to glass eel) and 448 days at estuarine arrival, with 98 days between metamorphosis and estuarine arrival. These ages were all significantly greater than those of American elvers 200, 55, and 255 days, respectively. Also, growth rate of the American eel (0.008 in [0.21 mm] per day) is greater than that of European eel (0.006 in [0.15 mm] per day). This is a result of delayed metamorphosis in the European species, which allows the European eel larvae to be transported from North America to Europe by the oceanic current. Thus, the European eel evolves the strategy to delay metamorphosis by reducing growth rate, enabling it to segregatively migrate with the American eel. The differences in leptocephalus stage duration and growth rate are the principal factors determining the segregation of migrating American and European eels.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The European eel is consumed fresh, dried or salted, or smoked, and it can be fried, boiled, and baked. It is particularly popular among Mediterranean Europeans. This species has been raised by the aquaculture industry, particularly in Japan and Taiwan, with some success. ◆

American eel
Anguilla rostrata

FAMILY
Anguillidae

TAXONOMY
Muraena rostrata Lesueur, 1817, Cayuga Lake, New York.

OTHER COMMON NAMES
English: Common eel; French: Anguille américaine; German: Amerikanischer Aal; Spanish: Anguila Americana.

PHYSICAL CHARACTERISTICS
Males grow to 59.84 in (152 cm) and females to 47.24 in (120.0 cm); these eels weigh as much as 16.16 lb (7.330 kg). The major difference between the European eel and the American eel is the number of vertebrae, which is 110 to 119 and 103 to 111, respectively. Otherwise, the species are almost identical.

DISTRIBUTION
Western Atlantic from Greenland and the Atlantic coast of Canada and the United States to Panama and throughout much of the West Indies south to Trinidad. The range includes the Great Lakes, the Mississippi River, and the Gulf basin. It has been introduced to Guam and Japan.

HABITAT
At sea they are found over rather deep waters; in freshwater they are inhabit permanent streams with continuous flow.

BEHAVIOR
Individuals of this species are solitary and nocturnal. While in freshwater, they hide during the day in undercut banks and in deep pools near logs and boulders and sometimes bury themselves in the substrate, whether mud, sand, or gravel. At night they typically swim near the bottom in search of food. They can breathe through the skin along with their gills and are able to live for several hours outside water.

FEEDING ECOLOGY AND DIET
Like the European eel, food items vary with the stage of development and location. The leptocephalus larvae, for example, is planktivorous; the elver feeds on aquatic insects, small crustaceans, and dead fish; and the adult eats insects, crustaceans, clams, worms, fish, frogs, toads, and dead animal matter. Sharks are their main predator.

REPRODUCTIVE BIOLOGY
Despite many attempts to conduct direct observations, knowledge of reproductive behavior can only be inferred, based on circumstantial evidence. We know that during the autumn adults migrate to the Sargasso Sea to spawn, with spawning taking place in January. At that time, females lay up to four million buoyant eggs, dying shortly after. After fertilizing the eggs, the males also die. With the help of ocean currents, the leptocephalus larvae drift toward coastal waters for as long as 18 months. After becoming an elver, American eels undergo a slow transformation that includes increases in their size, eye diameter relative to body size, and in the amount of eye pigments. They also become darker along the body. They spend most of their lives (up to 20 years) in freshwater before returning to the sea for spawning.

CONSERVATION STATUS
Not listed by the IUCN. It has been listed as "rare" by a number of U.S. counties and states, but lacks specific legislation to protect it. Nonetheless, fishery authorities in the United States are taking measures to decrease the impact of fisheries, particularly at the larval and elver level. The Atlantic States Marine Fisheries Commission is preparing a Fishery Management Plan (FMP), requesting that the U.S. federal government include this species under some protection status under the supervision of the U.S. Fish and Wildlife Service.

SIGNIFICANCE TO HUMANS
They are consumed as food and prepared in many ways. Larvae and elvers (considered a delicacy) are captured using fine

mesh fyke nets and dip nets; adults are caught with eel pots and trot lines. Although they can be caught in considerable numbers, their handling can be difficult, because the adults exude a noticeable layer of slime over the entire body. Moreover, large eels actively bite when caught on a hook and line. ◆

Froghead eel
Coloconger raniceps

FAMILY
Colocongridae

TAXONOMY
Coloconger raniceps Alcock, 1889, Bay of Bengal.

OTHER COMMON NAMES
Japanese: Fusa-anago.

PHYSICAL CHARACTERISTICS
May grow to 19.7 in (50 cm). The body is stubbier (particularly in the anterior region) than the bodies of most true eels. They have numerous pores in short tubes.

DISTRIBUTION
Indo-West Pacific area, from East Africa and Madagascar in the west to the western Pacific in the east to southern Japan in the north.

HABITAT
Deep-sea species usually found at depths between 980 and 3,720 ft (300–1,113 m).

BEHAVIOR
Because of its deep-water habits, it is rarely observed except very occasionally by deep sea submersibles.

FEEDING ECOLOGY AND DIET
Apparently feeds on other fishes.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

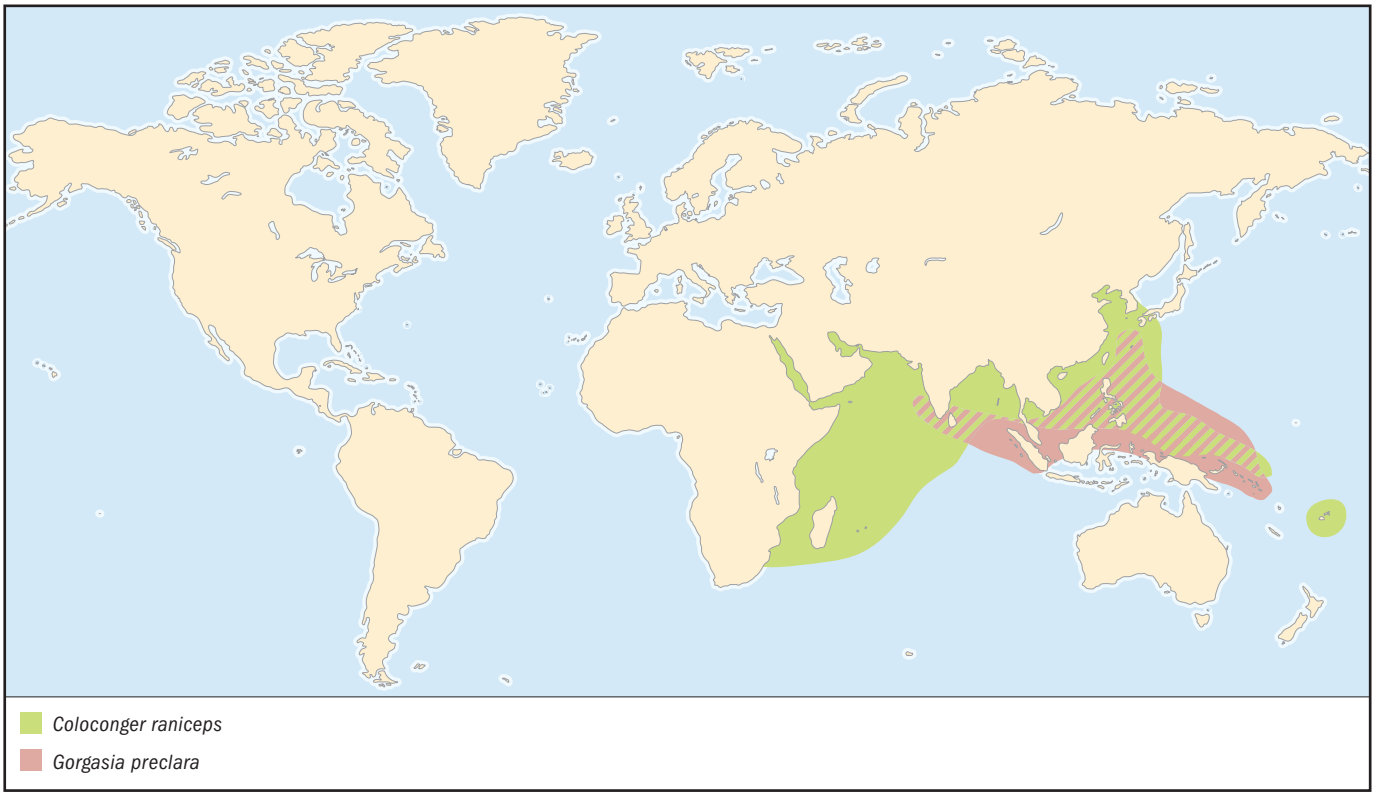
American conger
Conger oceanicus

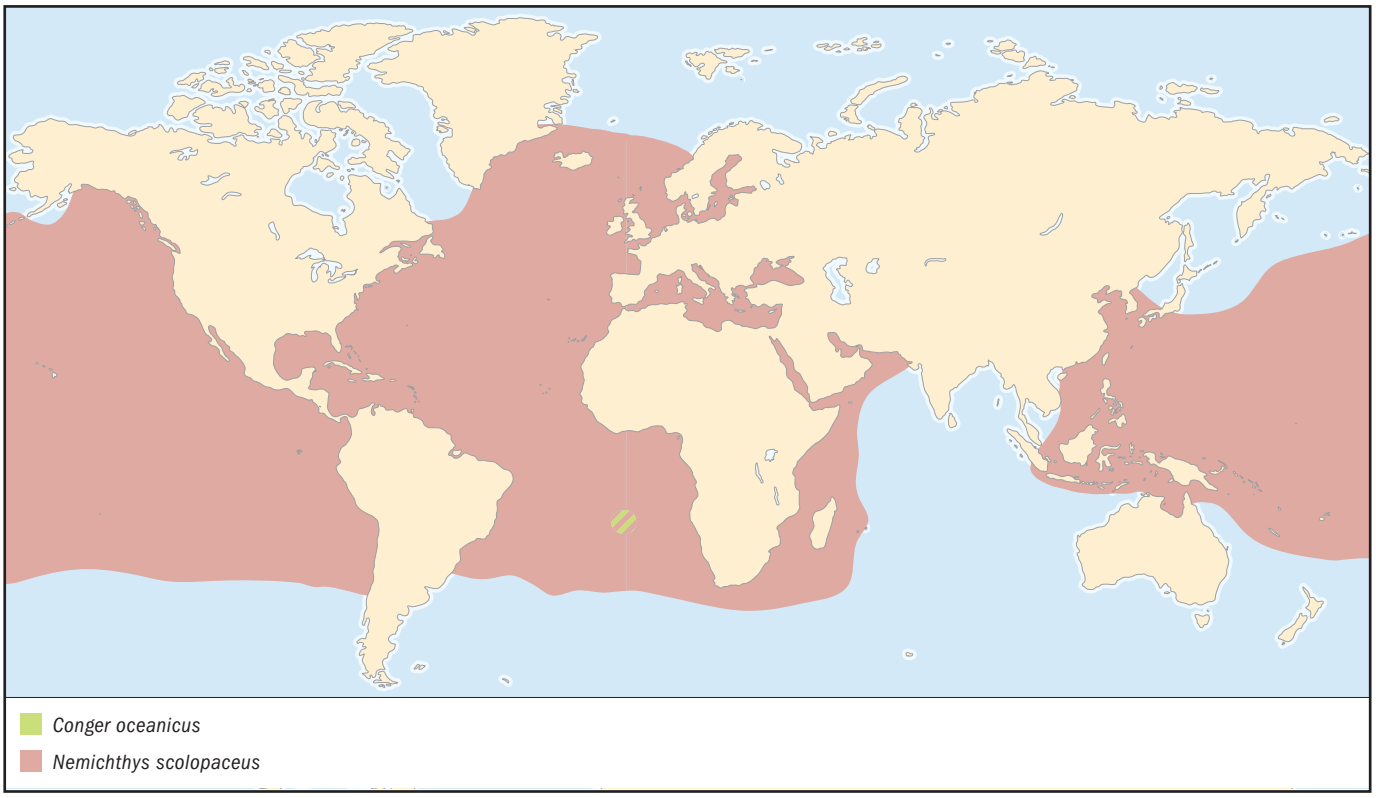
FAMILY
Congridae

TAXONOMY
Anguilla oceanica Mitchill, 1818, Atlantic.

OTHER COMMON NAMES
English: Conger eel, sea eel; French: Congre d'Amérique; Spanish: Congrio americano.

PHYSICAL CHARACTERISTICS
Specimens may reach 90.6 in (230 cm) and 88.2 lb (40 kg). The species has a long snout and a very large dorsal fin that originates much closer to the pectoral fins. It is gray on the dorsum and white on the venter.





DISTRIBUTION
Western Atlantic from Cape Cod, Massachusetts, to northeastern Florida in the United States as well as in the northern Gulf of Mexico westward to the Mississippi delta. In the eastern Atlantic it has been reported around Saint Helena Island, South Carolina.

HABITAT
Usually inhabits shallow inshore waters to depths of 1,565 ft (477 m).

BEHAVIOR
Chiefly nocturnal feeder in shallow waters (60 ft [18 m] or less).

FEEDING ECOLOGY AND DIET
Feeds mainly on fishes but also on shrimps, worms, and other small benthic organisms.

REPRODUCTIVE BIOLOGY
Spawning occurs from June through August. The leptocephalus larva reaches a maximum length between 5.9 and 6.3 in (15–16 cm). Metamorphosis consists of thickening of the head and body and development of the swim bladder, permanent teeth, and pigment in the skin.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Anglers along piers, docks, and jetties in the mid-Atlantic states commonly catch this species. It is caught in baited fish and crab traps as well as on hook and line but seldom in nets, because the fish can squirm through them. It is difficult to remove them from hooks. They are marketed fresh and salted in the Chesapeake Bay region, but today the species is not subject to commercial fishing in the United States and is rarely eaten. American congers are much more appreciated in parts of Europe, Africa, and Asia, where they are smoked. ◆

Splendid garden eel
Gorgasia preclara

FAMILY
Congridae

TAXONOMY
Gorgasia preclara Böhlke and Randall, 1981, Sumilon Island, Philippines.

OTHER COMMON NAMES
English: Orange-barred garden eel.

PHYSICAL CHARACTERISTICS
Individuals may reach 15.75 in (40 cm) in length. They have slender and elongated bodies with short mouths, anterior nostrils on the snout tip between restricted labial flanges, and small pectoral fins. The number of vertebrae ranges from 144 to 156.

DISTRIBUTION
Indo-West Pacific region from the Maldives in the west to Papua New Guinea in the east and from the Philippines and Ryukyu Islands in the north to the Coral Sea in the south.

HABITAT
Found in colonies on sand slopes exposed to current at depths usually below 90 ft (30 m).

BEHAVIOR
Live individually in burrows, forming large colonies. They hover above their sand burrows and retreat tail first when disturbed.

FEEDING ECOLOGY AND DIET
They feed on plankton that they capture while standing in their burrows.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Rusty spaghetti eel
Moringua ferruginea

FAMILY
Moringuidae

TAXONOMY
Moringua ferruginea Bliss, 1833, Island of Mauritius.

OTHER COMMON NAMES
English: Slender worm-eel; Gela (Solomon Islands): Poli ni tahi.

PHYSICAL CHARACTERISTICS
May reach 55.1 in (140 cm) in length. It has a wormlike, very elongated body with yellow to reddish coloration. The dorsal and anal fins are reduced to low folds. It lacks scales and has greatly reduced eyes. The gill openings are low on the body. The rusty spaghetti eel has about 73 lateral-line pores before the anus.

DISTRIBUTION
Indo-Pacific, from East Africa in the west to Easter Island in the east and from the Ryukyu Islands in the north to Australia in the south. It is distributed throughout Micronesia as well.

HABITAT
Found in sandy bottoms.

BEHAVIOR
Fossorial in that it can burrow headfirst. The physical attributes, such as an elongated body and reduced eyes, allow for this behavior.

FEEDING ECOLOGY AND DIET
Feeds on small prey found either on the bottom or burrowed in the sand.

REPRODUCTIVE BIOLOGY
Little is known, except that rusty spaghetti eels seem to show sexual dimorphism in size and coloration.

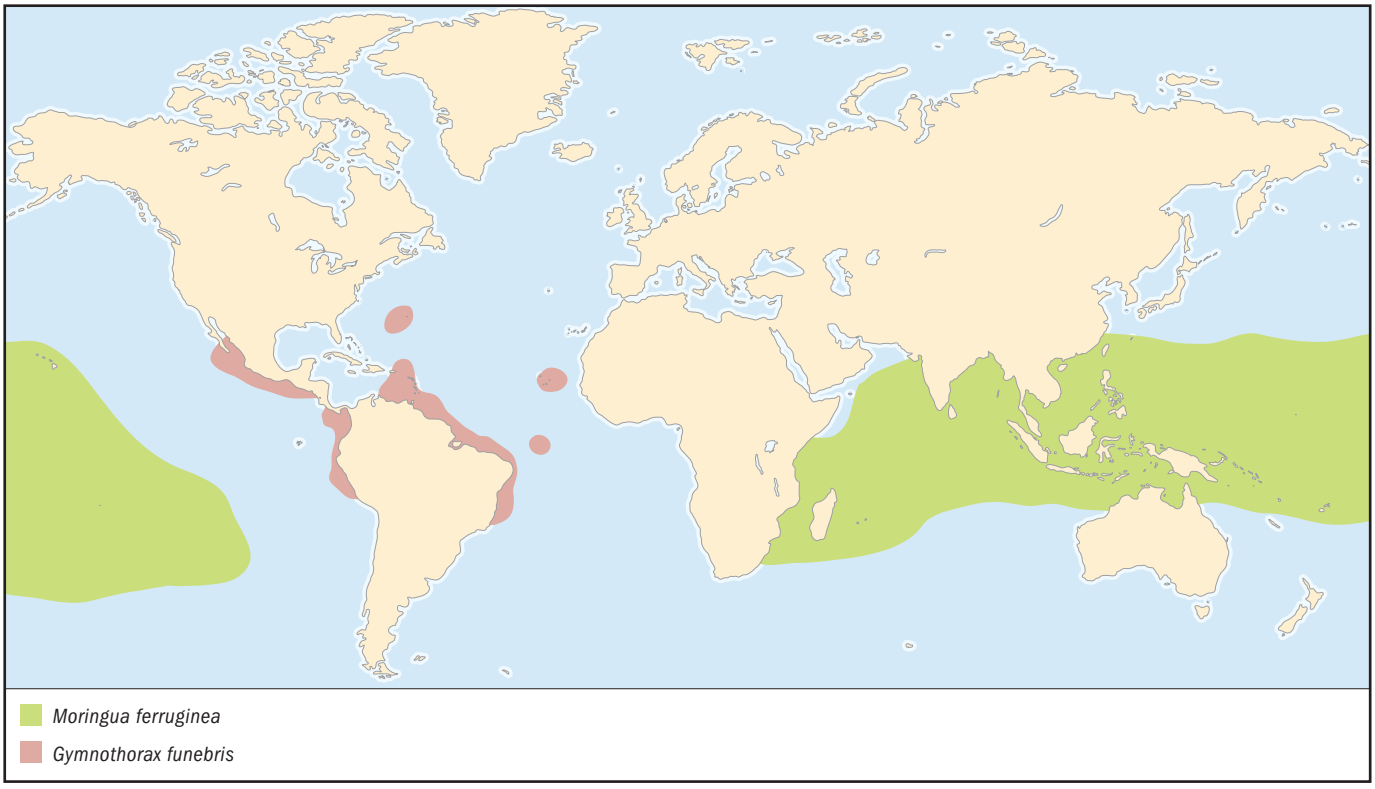
CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Green moray
Gymnothorax funebris

FAMILY
Muraenidae

TAXONOMY
Gymnothorax funebris and *Lycodontis funebris* Ranzani, 1840, Atlantic Ocean.



OTHER COMMON NAMES
English: Black moray; French: Murène verte; Spanish: Culebra morena.

PHYSICAL CHARACTERISTICS
Grows to 98.5 in (250 cm) in length and weighs up to 64 lb (29 kg). It is considered the largest Atlantic moray. Individuals of this species are uniformly greenish to dark gray-greenish. The green moray's color is a result of a yellowish mucous over the animal's dark blue skin.

DISTRIBUTION
Distributed throughout the western and eastern Atlantic (from Nova Scotia, Canada, to Brazil, including the Gulf of Mexico and Bermuda) and the eastern Pacific.

HABITAT
Benthic and solitary species commonly seen along rocky shorelines, reefs, and mangroves, including dirty harbors, in waters shallower than about 90 ft (about 30 m).

BEHAVIOR
Cleaned by some species of gobies and other fish species, as observed on the coral reefs in Bonaire and the Netherlands Antilles and at the Fernando de Noronha archipelago in the western South Atlantic.

FEEDING ECOLOGY AND DIET
Feeds on fishes and benthic crustaceans.

REPRODUCTIVE BIOLOGY
Little is known about reproduction, except that green morays have external fertilization and, like any other anguilliform, they have a leptocephalus larval stage.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Green morays are consumed as food and are marketed both fresh and salted. Large individuals are ciguatoxic, however. Ciguatera is a type of food poisoning caused by the consumption of tropical marine species that harbor a heat-resistant, acid-stable toxin known as ciguatoxin. The green moray consumes certain species of microorganisms that form this toxin. This natural toxin can concentrate as it moves up the food chain, but its adverse effects appear to be limited to humans. Because of its large size and aggressiveness, the bites of this moray are particularly dangerous. ◆

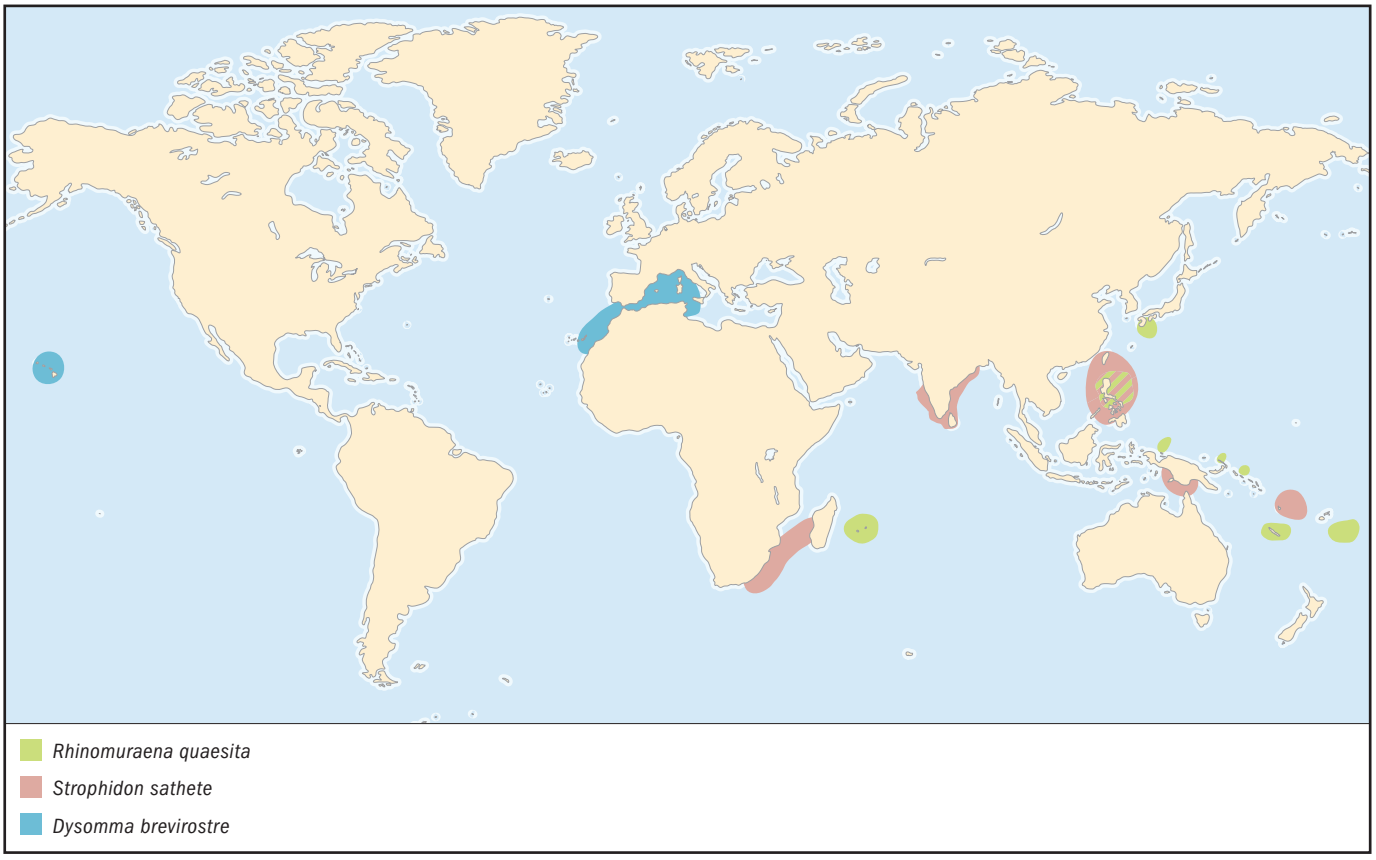
Ribbon moray
Rhinomuraena quaesita

FAMILY
Muraenidae

TAXONOMY
Rhinomuraena quaesita Garman, 1888, Marshall Islands.

OTHER COMMON NAMES
English: Ribbon eel, black ribbon eel; French: Rhinomurène noire; Samoan: Pusi.

PHYSICAL CHARACTERISTICS
May reach 51.2 in (130 cm) in length. It has a very elongated body. Mature males are mostly blue, whereas mature females



are almost completely yellow. They have three fleshy tentacles on the tip of the lower jaw; a single fleshy, pointed projection at the tip of the snout; and tubular anterior nostrils ending in gaudy, fanlike expansions.

DISTRIBUTION
Indo-Pacific from East Africa in the west to the Tuamotu Archipelago in the east and from southern Japan in the north to New Caledonia and French Polynesia in the south, including the Marianas and Marshall Islands in Micronesia.

HABITAT
Lagoons and associated seaward reefs as deep as 180 ft (60 m).

BEHAVIOR
Secretive, nonmigratory species that normally hides in sand or rubble, sometimes with only its head protruding.

FEEDING ECOLOGY AND DIET
Feeds on small fishes.

REPRODUCTIVE BIOLOGY
Fertilization in this species is external. This may be the only moray that undergoes abrupt changes in coloration and sex. It is classified as a protandrous hermaphrodite, that is, functioning males reverse sex to become females.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
It is acquired for display in aquaria because of its striking coloration and unusual morphological features. ◆

Slender giant moray
Strophidon sathete

FAMILY
Muraenidae

TAXONOMY
Muraenophis sathete Hamilton, 1822, Ganges River.

OTHER COMMON NAMES
English: Gangetic moray, giant estuarine moray; French: Murène fil géante; German: Süsswassermuräne; Spanish: Morenilla gigante; Tagalog (Philippines): Payangitan.

PHYSICAL CHARACTERISTICS
Specimens as large as 157.5 in (400 cm) have been recorded. Individuals of this species have a very elongated body. This species is brownish-gray dorsally and paler on the venter.

DISTRIBUTION
Indo-West Pacific Ocean, from the Red Sea and East Africa to the western Pacific.

HABITAT
Benthic muddy environments of marine and estuarine areas, including inner bays and rivers.

BEHAVIOR
The most interesting behavioral feature of this species is their ability to stand vertically from a burrow with the head kept horizontally beneath the surface, rising and falling with the tide.

FEEDING ECOLOGY AND DIET
Feeds on a wide variety of crustaceans and fishes.

REPRODUCTIVE BIOLOGY
Almost nothing is known about reproduction.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is consumed in India, the Philippines, Sri Lanka, South Africa, and other southeastern African countries as well as in Oceania. ◆

Slender snipe eel
Nemichthys scolopaceus

FAMILY
Nemichthyidae

TAXONOMY
Nemichthys scolopacea Richardson, 1848, type locality not available.

OTHER COMMON NAMES
English: Atlantic snipe eel, glass snake, threadfish; French: Avocette ruban; Spanish: Pez agazadicha.

PHYSICAL CHARACTERISTICS
Grows to 51.2 in (130 cm). They are extremely long eels whose posterior end is exceptionally narrow, to the point that it ends as a long filament. They have exceptionally long jaws that curve outward and do not close together except among fully mature males. They are also unusual because of their proportionally very large eye. In color they vary between dark brown and gray, often darker ventrally, with the anal fin and tips of the pectoral fins almost black. Males are quite different from females in that once they fully develop, their jaws shorten, and they lose their teeth. This feature led some researchers to believe that each sex was a separate species.

DISTRIBUTION
Worldwide in tropical and temperate seas. In the western Atlantic they range from Nova Scotia in Canada to the northern Gulf of Mexico and all the way south to Brazil. In the eastern Atlantic they are found from Spain to South Africa, including the western Mediterranean, although there are some reports from Iceland. In the northwestern Pacific they inhabit Japanese waters and the Arafura Sea. In the eastern Pacific they occur from Alaska to Chile, including the Gulf of California.

HABITAT
Pelagic, found mostly in middle to deep waters between 295 and 6,560 ft (91–2,000 m). The depth varies with the latitude—they occur in shallower waters at higher latitudes.

BEHAVIOR
As with many planktonic organisms, it is possible that their extremely elongated bodies are used to increase drag and therefore buoyancy in midwaters.

FEEDING ECOLOGY AND DIET
Feed on crustaceans while swimming with their mouths open.

REPRODUCTIVE BIOLOGY
They are oviparous, with external fertilization, buoyant eggs, and planktonic leptocephalus larva. The leptocephalus larva is

very elongated, with a filiform tail. The strong sexual dimorphism in the direction of degenerative changes in males and females suggests that they may display semelparity, that is, that they breed only once and then die immediately.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Tiger snake eel
Myrichthys maculosus

FAMILY
Ophichthidae

TAXONOMY
Muraena maculosa Cuvier, 1816, Mediterranean Sea.

OTHER COMMON NAMES
English: Ocellated snake eel, spotted snake eel; Afrikaans: Swartogies-slangpaling; Tahitian: Puhi popooru.

PHYSICAL CHARACTERISTICS
Specimens may reach 39.4 in (100 cm). The young have black saddles. Adults are pale cream in color, with large and small black spots. All have a stiffened, pointed tail.

DISTRIBUTION
Indo-Pacific region from the Red Sea and East Africa in the east to the central Pacific in the west. The species does not occur in the Hawaiian islands, where it has been replaced by *M. magnificus.*

HABITAT
Sandy areas of reef flats, lagoons, and seaward reefs. Lives buried in the sand.

BEHAVIOR
The most interesting behavioral characteristic of tiger snake eels is their ability to burrow tail first and then move equally forcefully forward and backward through the sediment. They may aggregate in large numbers under a light at night.

FEEDING ECOLOGY AND DIET
Feeds on small fishes and invertebrates.

REPRODUCTIVE BIOLOGY
Nothing is known.

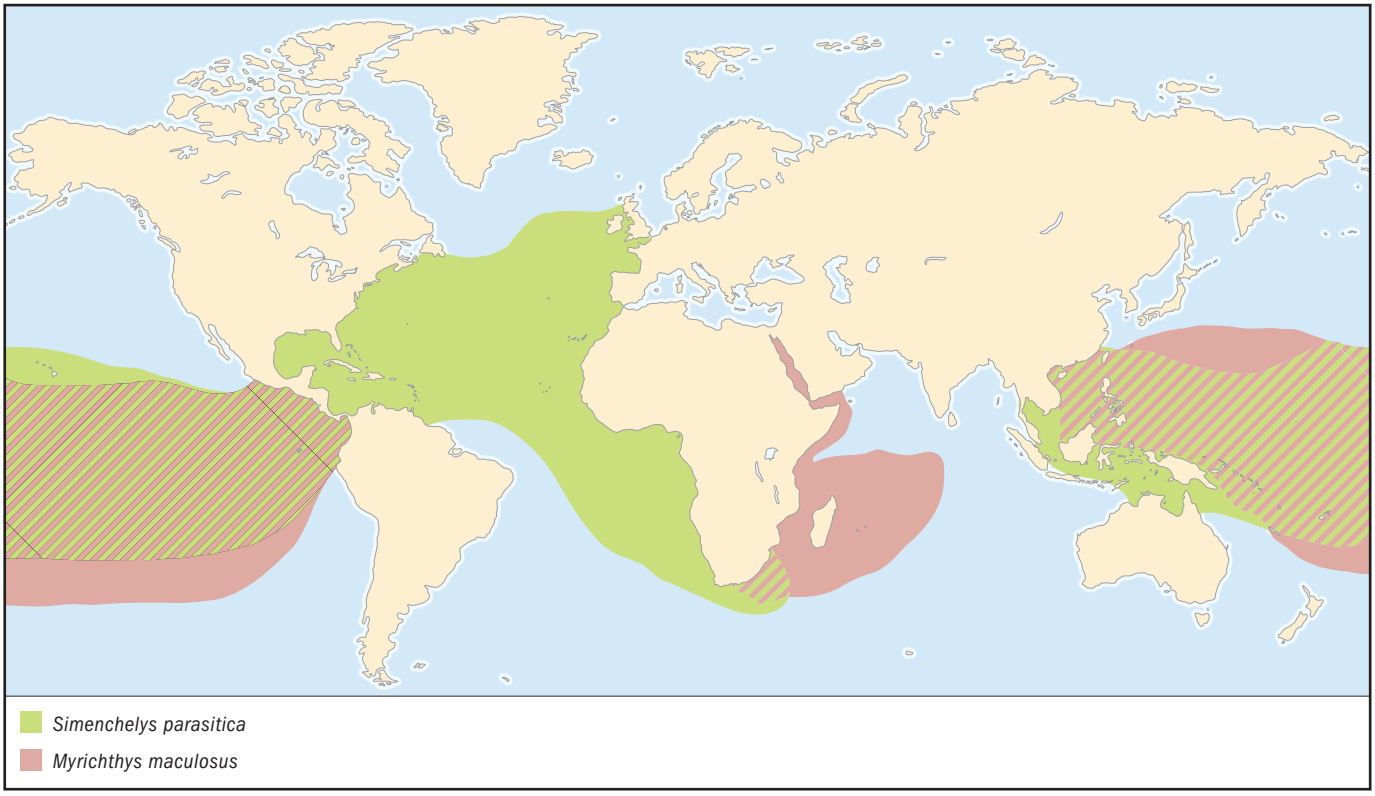
CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Pignosed arrowtooth eel
Dysomma brevirostre

FAMILY
Synaphobranchidae

TAXONOMY
Nettastoma brevirostre Facciolà, 1887, Sicily, Italy.



OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Individuals reach 11.8 in (30 cm) in length. Like most deep-sea fishes, they are pale in coloration. This species lacks pectoral fins as well as scales. The lower jaw is shorter than the upper jaw. It has between 193 and 204 vertebrae.

DISTRIBUTION
North Atlantic, from Madeira to the Gulf of Guinea, including the western Mediterranean. It is found all the way to Messina in Sicily. It also occurs off the coasts of Florida in the United States and has been recorded in Hawaii.

HABITAT
Muddy substrates of waters at a depth range between 1,150 and 2,130 ft (350–650 m).

BEHAVIOR
Burrowing, solitary species.

FEEDING ECOLOGY AND DIET
Probably feeds on small benthic fish and invertebrates.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Snubnosed eel
Simenchelys parasitica

FAMILY
Synaphobranchidae

TAXONOMY
Simenchelys parasitica and *S. parasiticus* Gill, 1879, Massachusetts.

OTHER COMMON NAMES
English: Slime eel; French: Anguille à nez court.

PHYSICAL CHARACTERISTICS
Specimens may reach 24 in (61 cm). This species has a slimy body with a blunt, thick, round snout and a small mouth. The gill slits are broadly separated, and the scales are embedded in the skin. Coloration is gray to grayish-brown; it is darker on the fin edges and along the lateral line.

DISTRIBUTION
Worldwide species, particularly in tropical and subtropical waters.

HABITAT
Individuals of this species are found at depths of 1,200–8,700 ft (365–2,650 m), over muddy, deep-sea bottoms. They also parasite on other fishes.

BEHAVIOR
Little is known besides their feeding behavior. They are capable of homing in on dead animals.

FEEDING ECOLOGY AND DIET
Feeds on benthic invertebrates and fish, including dead tissue. It is parasitic on some fishes. Large, dead fishes may look as if they are alive as these eels feed inside their carcasses.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
No significant economic importance but are of scientific value because their unusual ecological characteristics and feeding habits.

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Aldemaro Romero, PhD

Saccopharyngiformes
(Swallowers and gulpers)

Class Actinopterygii
Order Saccopharyngiformes
Number of families 4

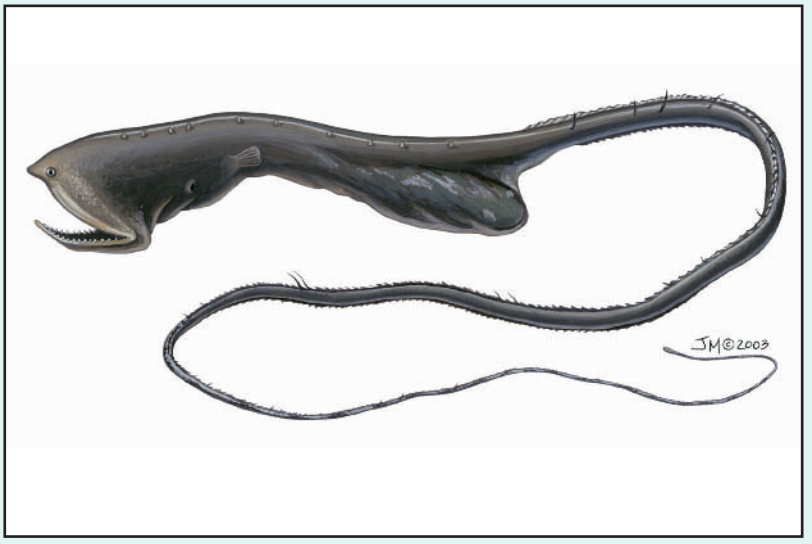


Illustration: Gulper eel (*Saccopharynx ampullaceus*). (Illustration by Jacqueline Mahannah)

Evolution and systematics

The Saccopharyngiformes are divided into two suborders, the Cyematoidei, with the single family Cyematidae (with two monotypic genera), and the Saccopharyngoidei, which contains the other three families. Of these three families, the Monognathidae is the most diverse, with 14 identified species in the genus *Monognathus*. The Saccopharyngidae has 11 species in the single genus *Saccopharynx*; the closely related family Eurypharyngidae is monotypic. There is still controversy over the inclusion of the Cyematidae in this order, but they are placed here on the basis of reduction of skeletal features that are common among all four families. Systematists consider the Saccopharyngiformes to be quite different from anguilliform eels. The order is thought to consist of highly specialized fishes. All four families share numerous common features, most of which have to do with extreme loss of skeletal features, presumably the result of the extremely energy poor environment.

Within the Saccopharyngoidei, the eurypharyngids and saccopharyngids are superficially most similar in appearance and are considered the closest in taxonomic relationship. The Monognathidae represent a more advanced and highly specialized family, as evidenced by even greater reduction in skeletal components, that is, the loss of the upper jaw. The first fossil evidence for this order is reported to be from the Middle Cretaceous.

Physical characteristics

The loss of skeletal structures has resulted in fishes that are among the most unusual and striking in their appearance. Among other characteristics, all are scaleless, lack pelvic fins, and have very long dorsal and anal fins. All are rather "flabby" to the touch and presumably are very poor swimmers. In members of the Saccopharyngoidei, the mouths are very large to enormous, with distensible pharynges and stomachs, to allow for the capture of very large prey. Dentition varies among the families. Well-produced, posteriorly curved teeth are found in the Saccopharyngidae, with the other three families possessing small to minute teeth in the jaws.

Except for the enlarged head and mouth structure, the rest of the body of these fishes is elongated and very slender (filamentous in eurypharyngids and saccopharyngids). The body coloration varies from scattered pigment patches to a light uniform brown in monognathids, with dark brown to solid black in cyematids, eurypharyngids, and saccopharyngids. Thin white lines of unknown function extend from the head to the tail along the upper body in the saccopharyngids and eurypharyngids, and individuals in both families have luminous bulbs at the very tip of the filamentous tail. The filament may constitute 50% or more of the overall length of the fish. Overall lengths of the substantial part of the body in all saccopharyngiforms is small, not exceeding 19.6 in (50 cm).

Distribution

Saccopharyngids are most abundant and diverse in the Atlantic Ocean. *Eurypharynx pelecanoides* is well known from the Atlantic and central and eastern Pacific Oceans, and the monognathids are about equally diverse in the Atlantic (six species) and Pacific Oceans (seven species). Among the Cyematidae, *Cyema atrum* is widespread in the Atlantic, Pacific, and Indian Oceans, while *Neocyema erythrostoma* is only known from the eastern South Atlantic. Saccopharyngiformes have not been reported from the Mediterranean.

Habitat

These are primarily bathypelagic inhabitants, with the majority of adult specimens being collected at depths greater than 3,280 ft (1,000 m). Larvae and juveniles live in shallower waters, even into the upper mesopelagic zone below 656 ft (200 m).

Behavior

Owing to the extreme depths at which these fishes live, there are few reports of any behavior.

Feeding ecology and diet

All saccopharyngiform species are poor swimmers at best. There have been no reports on feeding in the cyematids, but it is thought that eurypharyngids and saccopharyngids draw prey close to them by means of luminescent lures on their tails and then quickly open their mouths to suck food in. Saccopharyngids are piscivorous (eat only other fish); eurypharyngids take a broader range of fish and invertebrate prey. An even more unusual form of feeding has been postulated for monognathids. It is thought that their prey (crustaceans) may be lured by scent released from glands around the mouth; when they come close enough, the fish bite them by means of a hollow fang in the mouth that injects venom, much like a rattlesnake. The fish then swallows the dead or dying shrimp whole. Little is known about the predators that feed in members of this order.

Reproductive biology

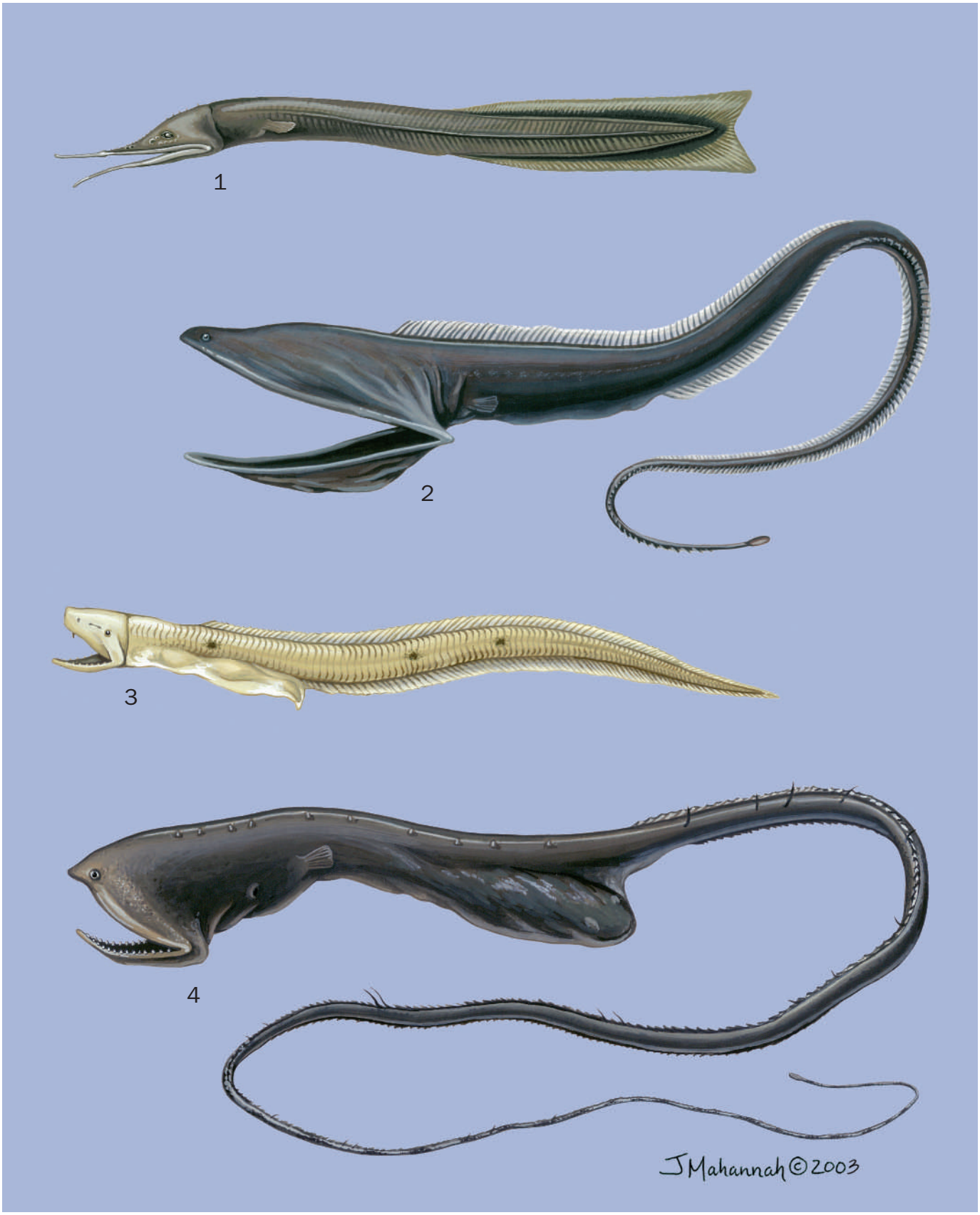
Nothing is known about the cyematoids, other than that they have separate sexes that do not appear to exhibit dimorphism. They also have leptocephalus larvae—a thin, largely transparent, ribbonlike stage that is common to several primitive orders of bony fishes (Elopiformes and Anguilliformes), including all saccopharyngiforms. In all three families of saccopharyngoids, sexually mature individuals are dimorphic. Males have greatly enlarged nasal structures and slightly enlarged eyes, and the jaws and stomachs in both males and females atrophy. It is widely believed that males locate their mates by following scent trails of pheromones released by the females and that spawning is a terminal event, with both individuals dying after mating. This reproductive pattern has been found in a number of shallow water eels and other fish species.

Conservation status

There are no known conservation measures specific to these families. No species from either family is listed on the IUCN Red List.

Significance to humans

Owing to their rarity and poorly studied biological characteristics, no significance can be attributed to saccopharyngiforms. They are objects of curiosity because of their extreme body specializations.



1. Bobtail snipe eel (*Cyema atrum*); 2. Pelican eel (*Eurypharynx pelecanoides*); 3. *Monognathus rosenblatti*; 4. Gulper eel (*Saccopharynx ampullaceus*). (Illustration by Jacqueline Mahannah)

Species accounts

Bobtail snipe eel
Cyema atrum

FAMILY
Cyematidae

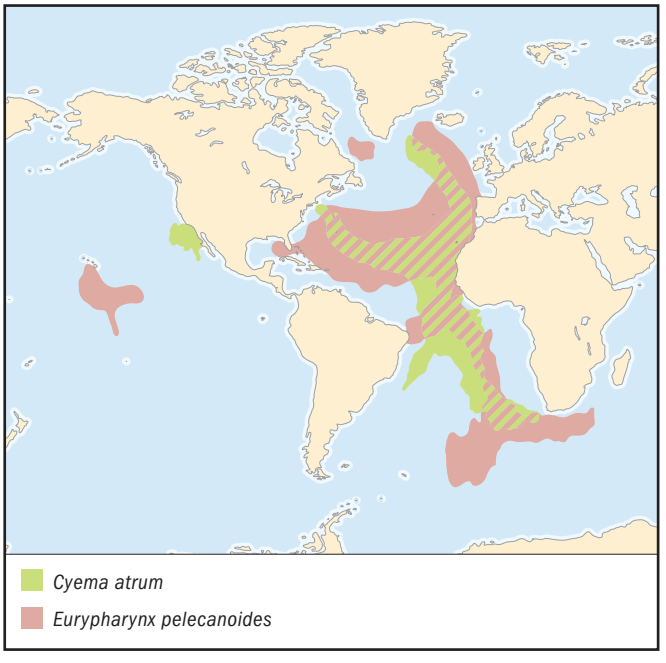
TAXONOMY
Cyema atrum Günther, 1878, South Pacific, Challenger station 1,770 ft (539 m); Antarctic, Challenger station 948; 9,000; and 10,800 ft (289; 2,743; and 3,292 m).

OTHER COMMON NAMES
English: Bobtail eel, deepwater eel; Danish: Korthalet ål; Finnish: Nuoliankerias.

PHYSICAL CHARACTERISTICS
This species has a rather striking appearance that is quite different from that of other saccopharyngiforms. Adults are black in coloration. This species is scaleless, like all members of the order. The eyes are very small. The jaws are thin and long, with numerous very fine teeth, and the jaws curve slightly away from each other at their tips. The dorsal and anal fin rays become progressively more elongated toward the rear of the body and extend well past very short caudal rays; the effect is that in side view the fish looks like an arrow! It is a small species, with a maximum reported size of about 6.3 in (160 mm).

DISTRIBUTION
It has been reported from all oceans between about 70° north and 55° south. Most collections have been from the Atlantic and Pacific Oceans.

HABITAT
The species is oceanic, lower mesopelagic to bathypelagic. Although it has been reported from collections made as shallow as 1,148 ft (350 m), most records are from depths exceeding 4,921 ft (1,500 m).



BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
There has been little research on the feeding habits of this eel. Because of its jaw structure, it is suggested that the species feeds on comparable prey types and in a fashion similar to that of the anguilliform eels of the family Nemichthyidae, commonly known as snipe eels. Nemichthyids use their thin, recurved jaws to feed on crustacean shrimps, especially those in the family Sergestidae. Predators of this species are unknown.

REPRODUCTIVE BIOLOGY
Unlike the other saccopharyngiforms, there is no apparent sexual dimorphism in adults. No other reproductive data have been reported for this species. The leptocephalus stage is rather distinctive; the deep oval body has a very small pointed head and a pointed caudal extension. These features grow a bit larger than in other saccopharyngiform leptocephali, with a maximum recorded total length of 2.8 in (70 mm).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Pelican eel
Eurypharynx pelecanoides

FAMILY
Eurypharyngidae

TAXONOMY
Eurypharynx pelecanoides Vaillant, 1882, off New England, United States, about 40°N, 68°W, 3 Albatross stations, 2,334–8,802 ft (711–2,683 m).

OTHER COMMON NAMES
English: Big mouth gulper eel, pelican gulper, pelican gulper fish, pelican fish, deep-sea gulper, umbrella mouth gulper; French: Grand-gousier pelican; German: Pelikanaal; Spanish: Pez pelicano; Danish: Pelikanål; Finnish: Pelikaaniankerias; Icelandic: Gapaldur; Japanese: Fukuro-unagi; Polish: Polykacz.

PHYSICAL CHARACTERISTICS
Superficially similar to species in the genus *Saccopharynx*, with which it shares the closest taxonomic relationship within the order, this species is coal black overall, except for a tiny white region on the caudal organ. It is scaleless. Probably the most striking differences between the pelican eel and *Saccopharynx* species are that the jaw length is extreme, almost 50% of the distance to the anus; the jaw teeth are very small; and there is a gradual narrowing of the body posterior to the abdomen. Other similarities to *Saccopharynx* species include small eyes that detect light rather than form visual images, the presence of a presumably luminous caudal organ at the end of a very long filamentous tail, an expansible stomach, and a weakly ossified and poorly muscled body. Because the delicate tail is usually broken, the maximum size is uncertain, but the largest

intact specimen ever collected measured 25.9 in (750 mm) in total length.

DISTRIBUTION
This a circumglobal species, found in temperate and tropical waters of all oceans. It is best known from the Atlantic and eastern and central Pacific Oceans.

HABITAT
The species is oceanic and bathypelagic. Although there are some shallow-water capture records at less than 1,640 ft (500 m), most individuals are collected between 3,281 and 9,842 ft (1,000–3,000 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
This species takes in a wider range of prey than do species in the genus *Saccopharynx*. Prey items include fishes, various crustaceans (especially caridean decapod shrimps), and cephalopod mollusks. In addition, there have been several reports of benthic prey items in the stomachs of pelican eels. Predators are unknown.

REPRODUCTIVE BIOLOGY
Reproduction is similar to that of species in the genus *Saccopharynx*, in that sexually mature males have greatly expanded nasal structures, accompanied by stomach atrophy, loss of dentition, and reduction in jaw structure. Reproduction is apparently a terminal event. Leptocephalus larvae are oval and deep-bodied, like *Saccopharynx* species, but they are smaller, with a maximum length of about 1.6 in (40 mm). They have several greatly elongated larval teeth in the upper jaw.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Monognathus rosenblatti

FAMILY
Monognathidae

TAXONOMY
Monognathus rosenblatti Bertelsen and Nielsen, 1987, Central North Pacific, 31°N, 159°W, 14,300–17,300 ft (4,853–5,266 m)—bottom is 19,000 ft (5,800 m).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The monognathids are truly bizarre in appearance. Probably the two most striking features are the complete lack of an upper jaw (which gives the family its name) and the presence of a hollow rostral fang that extends downward from the roof of the mouth. The fang is associated with a glandular mass thought to secrete venom. The body is scaleless, very slender, and pale tan to light brown in color. As with other saccopharyngoids, the eyes are very small, the stomach is distensible, the body skeleton is poorly ossified, and the musculature is weak. The caudal region is flattened laterally but does not extend into the long filament seen in saccopharyngids and eurypharyngids. Monognathid species have been divided into two groups based on the relative shape and length of their skulls; there is a "short-skulled" group and a "long-skulled" group, with *M. rosenblatti* belonging to the latter. The largest specimen collected measured 2.8 in (70 mm) in length, although the largest monognathid reported thus far was 11.4 in (290 mm).

DISTRIBUTION
This species is known only from the northeastern Pacific Ocean.

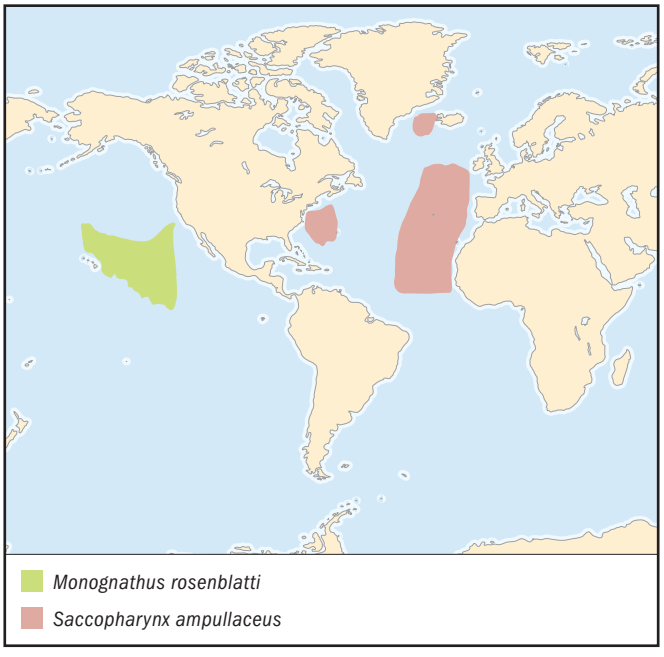
HABITAT
As with others in this genus, this species is found in oceanic, deep bathypelagic habitats. The shallowest record for *M. rosenblatti* is 6,889 ft (2,100 m). Due to their habitat, this family is exceptionally rare. All 14 species are known form a combined total of fewer than 80 individuals, about 50% of which belong to *M. rosenblatti*.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
No stomach contents have been reported from any *M. rosenblatti* specimens, but prey from other monognathid species have all been crustacean shrimps. All of the shrimps were quite large relative to the body size of the fish. It has been hypothesized that these weak fish inject their prey with venom using the rostral fang, in much the same fashion as certain venomous snakes overcome their prey. Predators are unknown.

REPRODUCTIVE BIOLOGY
As with the other saccopharyngoids, the sexually mature collected specimens of monognathids (none of which were *M. rosenblatti*) exhibit dimorphism and evidence that spawning is a one-time terminal event. Males possess greatly enlarged nasal structures, suggesting that locating of mates takes place by scent. Although it is believed that the larval form is a leptocephalus, as yet none has been positively identified as belonging to this family.

CONSERVATION STATUS
Not threatened.



SIGNIFICANCE TO HUMANS
None known. ◆

Gulper eel
Saccopharynx ampullaceus

FAMILY
Saccopharyngidae

TAXONOMY
Ophiognathus ampullaceus Harwood, 1827, NW Atlantic Ocean, 32°20'N, 30°16'W, 0–6,234 ft (0–1,900 m). Neotype: ISH 3288/79. Original locality 62°N, 57°W. Neotype selected by Nielsen and Bertelsen (1985).

OTHER COMMON NAMES
English: Pelican fish; Danish: Slugål; Finnish: Ahmattiankerias; Icelandic: Pokakjaftur; Polish: Gardzielec.

PHYSICAL CHARACTERISTICS
The body is attenuated and very flabby, with poorly ossified bones and weakly developed muscles. The most striking attributes are tiny eyes that function as light detectors; a greatly enlarged mouth with numerous slightly recurved teeth; an elongated stomach region, with the posterior end of the abdomen clearly demarcated from the tail, and an extremely long tail (about 75% of body length), with an elongated caudal filament that terminates in a "caudal organ" believed to be luminescent. Because of the delicacy of the body, the filaments often are broken off in captured specimens. The body is scaleless. The largest intact specimen measured 5.2 ft (1.6 m), although much of the body length consists of the elongated whiplike tail and caudal filament.

DISTRIBUTION
This species is the best known of the genus. It has been collected only from the North Atlantic Ocean between 10° and 65° north latitude.

HABITAT
The gulper eel is oceanic and bathypelagic. Only juveniles have been captured at depths of less than 2,624 ft (800 m). It is believed that adults typically reside deeper than 6,561 ft (2,000 m).

BEHAVIOR
Because of the great depths of its habitat, aspects of the behavior of this species are largely the subject of conjecture.

FEEDING ECOLOGY AND DIET
The species is piscivorous. Relatively few saccopharyngids have been recovered with intact stomach contents, but in all cases various fish species were the prey. The gulper eel has an extremely distensible stomach, allowing it to ingest very large prey. Because of its weak skeleton and body muscles, it is believed to be a very poor swimmer. It is thought to lure prey within range by means of the luminescent caudal organ, which it may suspend in the water near its mouth. The jaw muscles are the only well-developed muscles and probably allow the gulper eel to suck its prey into the large mouth by quickly opening the jaws. Predators are unknown.

REPRODUCTIVE BIOLOGY
Males and females are sexually dimorphic. Sexually mature males show extreme degeneration of the jaws, along with a loss of teeth and reduction in abdominal size. In addition, the eyes become somewhat enlarged, and the nasal apparatus is significantly enlarged. It has been suggested that males locate females by tracking pheromone (scent) trails released by the females. As with numerous eel species as well as some other deep-sea fish species, reproduction is thought to be a terminal event. As with eels in general, larval gulper eels have a leptocephalus, a ribbon-like transparent stage. Relatively few leptocephali have been collected, but all are deep-bodied and small, with a total length of 1.47–1.9 in (40–50 mm).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known.

Resources

Books

Bertelsen, E., Jørgen Nielsen, and David G. Smith. "Families Saccopharyngidae, Eurypharyngidae, and Monognathidae." In *Fishes of the Western North Atlantic*, edited by Eugenia B. Böhlke. Part 9. New Haven: Sears Foundation for Marine Research, 1989.

Nelson, Joseph S. *Fishes of the World.* 3rd edition. New York: John Wiley and Sons, 1994.

Smith, David G. "Order Saccopharyngiformes, Family Cyematidae." In *Fishes of the Western North Atlantic*, edited by Eugenia B. Böhlke. Vol. 9, Part 1. New Haven: Sears Foundation for Marine Research, 1989.

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Periodicals

Bertelsen, E., and Jørgen G. Nielsen. "The Deep-Sea Eel Family Monognathidae (Pisces, Anguilliformes)." *Steenstrupia* 13, no. 4 (1987): 141–198.

Gartner, John V. Jr. "Sexual Dimorphism in the Bathypelagic Gulper Eel *Eurypharynx pelecanoides* (Lyomeri: Eurypharyngidae), with Comments on Reproductive Strategy." *Copeia* 2 (1983): 446–449.

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Other

"FishBase: A Global Information System on Fishes." 7 Nov. 2002 (12 Nov. 2002). <http://www.fishbase.org/home.htm>

John V. Gartner Jr., PhD

Clupeiformes
(Herrings)

Class Actinopterygii
Order Clupeiformes
Number of families 5

Photo: A school of threadfin shad (*Dorosoma petenense*). (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Fishes in the order Clupeiformes are teleosts, a group of fishes characterized evolutionarily by the presence of true bone forming their skeletons and by specific bone structures in the tail and skull. Teleosts arose during the early Mesozoic era (approximately 200 million years ago). Four subsequent radiations gave rise to the current major groups of fishes, with one of these radiations producing the Clupeomorpha. A major evolutionary feature that distinguishes clupeomorphs is the extension of the gas bladder into the brain case so that it contacts the inner ear, and thereby increasing the hearing ability of the fish. Modern Clupeiformes also possess other evolutionary advances over their closest ancestors: a modified joint in the jaw caused by fusion of the angular to the articular and a reduction of the caudal skeleton.

Two suborders, Clupeoidei and Denticipitoidei, are recognized in the Clupeiformes. The Clupeiodei includes the families Chirocentridae (wolf herrings; 1 genus, 2 species), Clupeidae (herrings, menhadens, pilchards, sardines, shads, and sprats; 5 subfamilies, 56 genera, 214 species), Engraulidae (anchovies; 2 subfamilies, 16 genera, 145 species), and Pristigasteridae (sawbelly herrings; 2 subfamilies, 9 genera, 36 species). The Denticipitoidei includes the family Denticipitidae (denticle herring; 1 genus, 1 species).

Physical characteristics

Clupeoids are small fusiform (tapering toward each end) fishes with streamlined bodies that facilitate fast swimming in open water. They have dark shading on their backs and bright silvery sides. Except for the head, their bodies are completely covered in large scales. Most clupeoids lack a lateral line, and only in the deticipitoid herring does this line extend along the body. The fins of clupeoids lack spines. A single dorsal fin is located near the middle of the body, and the tail is forked. Many clupeoids have a row of scutes, modified scales that usually have sharp points towards the rear, along the medial line of the belly. The smallest cluepoid is the Sanaga pygmy herring (*Thrattidion noctivagus*), measuring only 0.83 in (2.1 cm) in standard length; male wolf herrings (*Chirocentrus* spp.) are the largest herring, attaining standard lengths of 39 in (100 cm).

Distribution

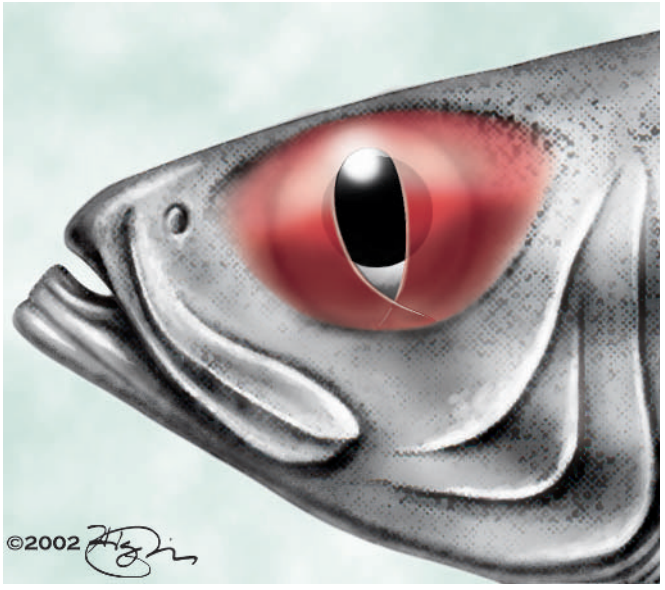
Clupeiformes are widely distributed worldwide between 70°N to 60°S latitude. They primarily live in oceans, but some species inhabit coastal margins and fresh water for at least a portion of their lives.

Habitat

Nearly all Clupeiformes are open-water, pelagic species. Four-fifths of all species are marine, with habitats ranging from nearshore littoral zones to nearly 100 mi (160 km) offshore. Many are found near the surface at times but often move to deeper waters during the day. Some Clupeiformes live in inland waters or are anadromous, moving inland to spawn. These species utilize bays, estuaries, marshes, rivers, and freshwater streams as habitats. Landlocked populations have formed as shads, alewives, and herrings moved into lakes or rivers and became trapped between dams.

Behavior

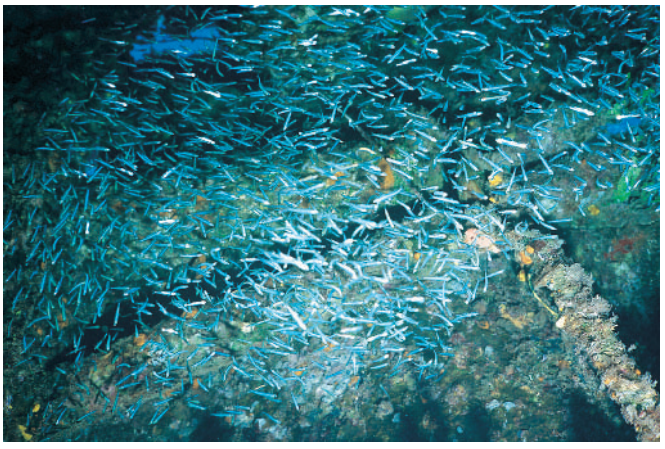
Clupeiformes are perhaps best recognized for the large schools they form. Schools may include hundreds or thousands of individuals ranging from the young to adults, but individuals in a school are usually of similar size. Schooling is



Some fish—mullets, jacks, mackerels, anchovies, and this herring, for example—have an adipose eyelid (highlighted here in red). Rather than being "fatty" as the name suggests, this immobile covering consists primarily of a matrix of extremely fine microfibrils of collagen. Its purpose is unknown. (Illustration by Jonathan Higgins)

a form of organization in which behavior is synchronized; large numbers of fish may swim parallel to each other in the same direction with fairly uniform spacing. These synchronized aggregations are believed to confer swimming efficiency and, most importantly, to enable fishes to avoid or deter predators. Clupeiformes also congregate in smaller, less-organized shoals, particularly during spawning seasons. In addition to schooling, many Clupeiformes undertake some type of migration. Some clupeoid fishes are anadromous, migrating from the ocean to streams and rivers for spawning. They also may migrate inshore or latitudinally on a seasonal basis. Many clupeoids migrate in the water column on a diel basis, staying at deep depths during the day and moving to shallow depths at night.

Northern anchovies (*Engraulis mordax*) swim in tightly packed schools. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)



A school of dwarf herrings (*Jenkinsia* sp.) swimming near Andros, Bahamas. (Photo by Jerry McCormick/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Most Clupeiformes filter feed by straining water through their long and numerous gill rakers. They consume plankton, particularly small crustaceans and the larval stages of larger crustaceans and fishes. Some herrings visually locate and target food particles. Clupeoid fishes are important prey for larger fishes, seabirds, and marine mammals.

Reproductive biology

Clupeiformes produce large numbers of offspring, either through a single seasonal spawning event or by spawning in seasonal peaks throughout the year. Most Clupeiformes spawn in shoals by broadcasting large numbers of small, buoyant eggs in waters near the surface. The eggs and larvae drift passively in currents as they develop. Herrings, on the other hand, produce demersal eggs that sink to the bottom, where they often adhere to the substrate until they hatch. After hatching, larvae become pelagic.

Conservation status

Two Clupeiformes are listed as Endangered by the IUCN: the Alabama shad (*Alosa alabamae*) and the Laotian shad (*Tenualosa thibaudeaui*). The Alabama shad is found in the northern portion of the Gulf of Mexico, from the Mississippi delta eastward to the Choctawhatchee River in Florida. It also occurs in inland rivers from Iowa to Arkansas and eastward to West Virginia. The Laotian shad occurs in the Mekong River basin, including inland waters of Thailand, Laos, and Cambodia. Most Clupeiformes are not threatened by severe population disruptions, but populations do show natural variability due to fluctuations in reproductive success. This natural variability is exacerbated by fishing pressure and global climate patterns.

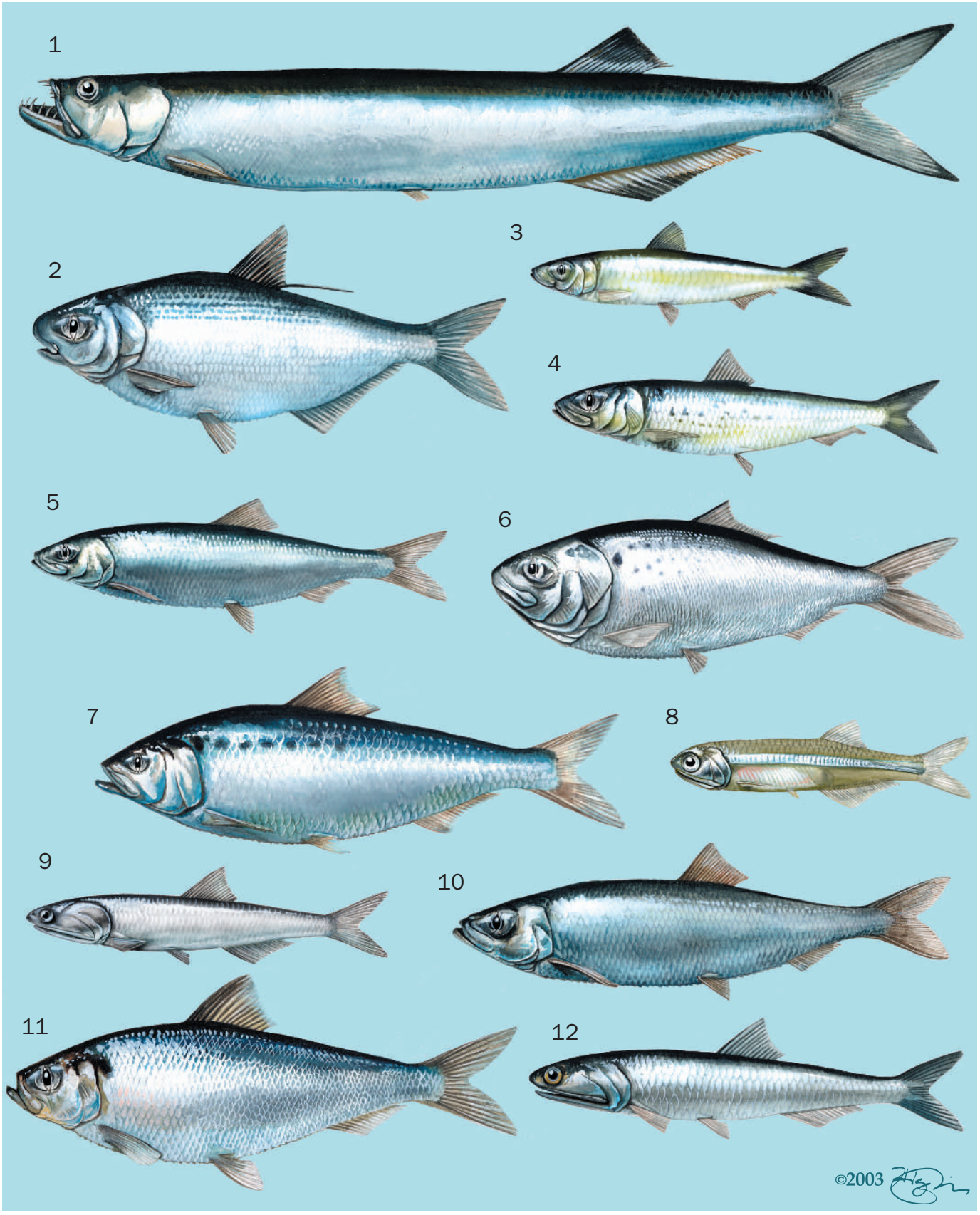
Significance to humans

Clupeiformes are some of the most economically important fishes in the world's oceans. They have been widely ex-

ploited throughout human history, primarily for food but also as a source of oil, fertilizer, and animal feed. Herring fishing was one of the earliest occupations of coastal peoples, as first described in England in a chronicle that dates back to A.D. 709. The first commercial fishing establishment opened in Heligoland, a small island in the North Sea off the coast of Germany, in 1425.

Clupeiformes continue to constitute a large portion of world's commercial fisheries. Although 186 species are exploited by pelagic fisheries worldwide, 50% of the total landings in 1997 were represented by only seven species. Among these seven, four are Clupeiformes: the anchoveta (*Engraulis ringens*), Atlantic herring (*Clupea harengus*), Japanese pilchard (*Sardinops melanostictus*), and South American pilchard (*Sardinops sagax*). Herrings and anchovies constitute approximately 25% of the total fisheries harvest worldwide.

In addition to being heavily utilized by humans, Clupeiformes are an important component of the broader marine ecosystem. They serve as food items for larger predatory fishes, sea birds, and marine mammals. Thus, clupeoids sustain other organisms of importance to humans through ecosystem interactions.



1. Dorab wolf herring (*Chirocentrus dorab*); 2. Gizzard shad (*Dorosoma cepedianum*); 3. European pilchard (*Sardina pilchardus*); 4. South American pilchard (*Sardinops sagax*); 5. Pacific herring (*Clupea pallasii*); 6. Atlantic menhaden (*Brevoortia tyrannus*); 7. American shad (*Alosa sapidissima*); 8. Bay anchovy (*Anchoa mitchilli*); 9. Northern anchovy (*Engraulis mordax*); 10. Atlantic herring (*Clupea harengus*); 11. Alewife (*Alosa pseudoharengus*); 12. Anchoveta (*Engraulis ringens*). (Illustration by Jonathan Higgins)

Species accounts

Dorab wolf herring
Chirocentrus dorab

FAMILY
Chirocentridae

TAXONOMY
Chirocentrus dorab Forsskål, 1775, Jiddah, Saudi Arabia.

OTHER COMMON NAMES
English: Blackfin wolf herring, dorab, silver barfish, wolf herring; French: Chirocentre dorab, sabre; German: Wolfshering; Spanish: Arencón dorab, arenque lobo de la India, sabre; Arabic: Gairi, kerli, dorab, samak abu sayf.

PHYSICAL CHARACTERISTICS
Reaches lengths of approximately 3.3 ft (1 m). Elongate, highly compressed body. Silvery with a bright blue-gray back. Unlike species of the Clupeidae, the wolf herring has no scutes along the belly. Two distinctive fang-like canine teeth point forward in the upper jaw, and a series of canine teeth is present in the lower jaw.

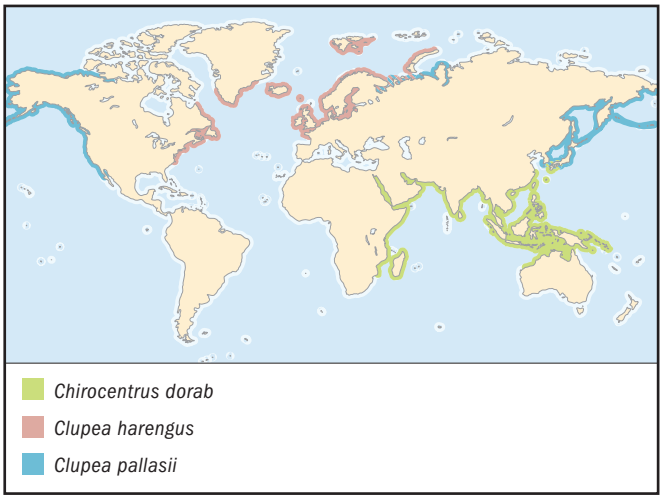
DISTRIBUTION
Warm coastal waters of the Indo-Pacific, from the Red Sea and East Africa, to the Solomon Island, north to Japan, and south to Australia.

HABITAT
Nearshore portions of oceans and inshore brackish areas.

BEHAVIOR
Does not form large schools, but a small number of individuals may be found together. Known for its leaping powers.

FEEDING ECOLOGY AND DIET
Feeds on other small schooling fishes, such as herrings and anchovies. To a lesser extent, it also eats fish eggs, larvae, and crustaceans.

REPRODUCTIVE BIOLOGY
Researchers believe that Dorab wolf herrings broadcast eggs into the water column, from which pelagic larvae hatch.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Minor commercial fishery in the Indo-Pacific, with products marketed fresh, frozen, dried, and salted. ◆

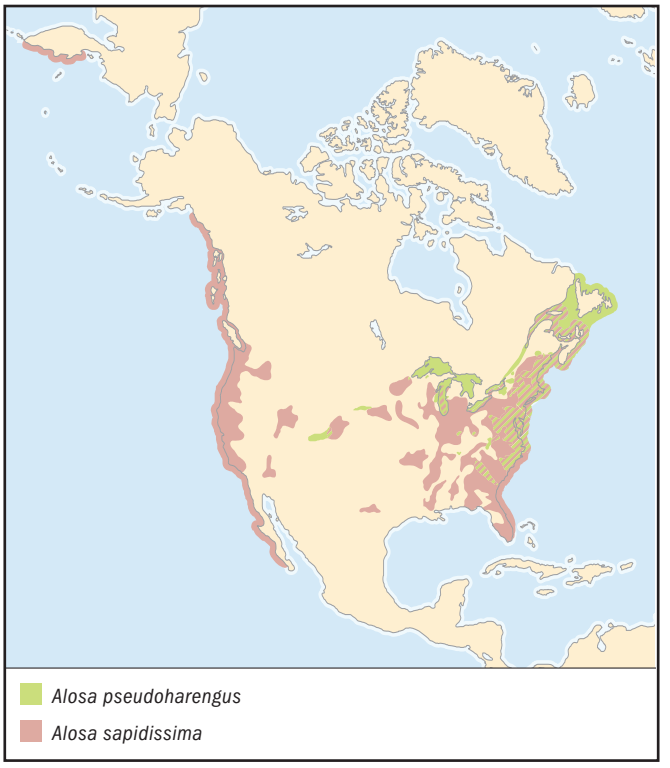
Alewife
Alosa pseudoharengus

FAMILY
Clupeidae

TAXONOMY
Alosa pseudoharengus Wilson, 1811, Delaware River at Philadelphia, Pennsylvania, United States.

OTHER COMMON NAMES
English: Bigeye herring, branch herring, freshwater herring, golden shad, grayback, gray herring, green shad, kyack, mulhaden, sawbelly, spring herring, white herring; French: Alose gaspareau, gaspareau, gasparot, gasperot; German: Maifisch; Spanish: Alosa, pinchagua.

PHYSICAL CHARACTERISTICS
Sea-run alewives reach a maximum length of 15 in (38.1 cm); landlocked alewives are typically around 6 in (15.2 cm). Small bodies. Strongly compressed laterally. Silvery bodies with grayish green backs. A row of scutes runs along the ventral edge of the belly. A single black spot is present behind the head.



DISTRIBUTION
Atlantic coast of North America, from the St. Lawrence River and Nova Scotia, Canada, to North Carolina. Numerous translocations of this species have resulted in the establishment of landlocked populations in many inland water bodies, including all of the Great Lakes.

HABITAT
Spends a large portion of its life at sea and migrates into inland freshwater streams for spawning. Landlocked populations live entirely in inland lakes or river systems.

BEHAVIOR
Forms schools in open water. Sea-run alewives migrate from the sea to freshwater streams to spawn. Populations in lakes migrate on a diel basis, moving inshore at night and retreating to deeper offshore waters during the day.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, primarily copepods, cladocerans, mysids, and ostracods. Inshore adults eat insect larvae as a large part of their diet.

REPRODUCTIVE BIOLOGY
Moves from the sea to rivers for spawning, with the timing of migration dependent on water temperature. In lakes, alewives move onto shallow beaches and into ponds to spawn. Males and females mature at one and two years of age, respectively. Females usually move to the spawning site before males. Groups of 2–3 fish spawn at night over gravel or rocky substrates. Eggs are broadcast by females and fertilized in the water column by males. Immediately after spawning, the eggs sink and adhere to the substrate. Upon hatching, the young remain at the spawning grounds until the late larval stage and then move slowly into deeper water or the sea.

CONSERVATION STATUS
Not listed by the IUCN, but overfishing, pollution, and impassable dams contribute to stock declines.

SIGNIFICANCE TO HUMANS
Harvested commercially and used as fresh, dried, or salted meat, bait for crab or lobsters, and sometimes as animal feed. Also serves as a forage base for other commercial or recreational fish stocks. In lakes, alewives can be a nuisance to humans. They may become so abundant that they clog industrial water intake pipes, and they often die off in massive events related to fluctuations in water temperature and dissolved oxygen. ◆

American shad
Alosa sapidissima

FAMILY
Clupeidae

TAXONOMY
Alosa sapidissima Wilson, 1811, Delaware River at Philadelphia, Pennsylvania, United States.

OTHER COMMON NAMES
English: Atlantic shad, common shad, Connecticut river shad, herring jack, North River shad, Potomac shad, Susquehanna shad, white shad; French: Alose, alose canadienne, alose savoureuse; German: Amerikanische Finte, Amerikanischer Maifisch; Spanish: Sábalo americano.

PHYSICAL CHARACTERISTICS
Average size 15 in (38 cm) long. Silvery with blue or blue-green metallic shading on its back. Moderately compressed body with a distinct keel of ventral scutes along the belly. A large black spot is located behind the rear edge of the gill cover, followed by several smaller dark spots.

DISTRIBUTION
Occurs off the Atlantic coast of North America, from the St. Lawrence River and Nova Scotia to central Florida. Introduced to the Sacramento River in California by the U.S. Fish Commission in 1971. Since then, its range has expanded greatly, and it can now be found from Cook Inlet, Alaska, to Baja, Mexico.

HABITAT
Occurs in the ocean at depths to 820 ft (250 m). As an anadromous fish, it spends most of its life at sea but migrates into estuaries and freshwater streams to breed.

BEHAVIOR
Forms schools after reaching a juvenile size of approximately 8–12 in (20–30 cm). Anadromous species, migrating into freshwater areas for spawning.

FEEDING ECOLOGY AND DIET
Planktonic feeder that consumes primarily copepods and mysids (shrimp-like crustaceans), but occasionally eats small fishes.

REPRODUCTIVE BIOLOGY
Ascends freshwater rivers and streams in the spring to spawn. Males mature at four years of age; females first spawn between five and seven years. Spawning commences at water temperatures of 53.6°F (12°C) and peaks at 65°F (18.3°C). The males arrive at the spawning location before the females. During spawning, several males and a female swim close to the surface during the evening. Females release eggs in the open water, where they are fertilized by males. Eggs are 0.1–0.15 in (2.5–3.5 mm) in diameter after fertilization, and after 8–10 days, small larvae of 0.35–0.40 after spawning, but juveniles spend their first summer in the river and reach the sea by autumn. Most American shad spawn more than once, but some die after spawning at southern latitudes of the Atlantic coast.

CONSERVATION STATUS
Not listed by the IUCN, but the presence of dams in rivers and streams impedes spawning migrations and has contributed to the decline of some populations.

SIGNIFICANCE TO HUMANS
Commercially fished in rivers and estuaries during spawning migrations. The flesh is eaten fresh, salted, or smoked, and this species is prized for its tasty roe. American shad play a central role in shad planking parties, where the fish are slow-cooked on oak boards over campfires. Shad planking parties are central to political rallies and community gatherings, particularly in the mid-Atlantic region of the United States. ◆

Atlantic menhaden
Brevoortia tyrannus

FAMILY
Clupeidae

TAXONOMY
Brevoortia tyrannus Latrobe, 1802, Chesapeake Bay, United States.

OTHER COMMON NAMES
English: Bony fish, bugfish, bunker, fatback, menhaden, mossbunker, pogy, whitefish; French: Alose tyran, menhaden tyran, menhaden; German: Menhaden; Spanish: Lacha tirana.

PHYSICAL CHARACTERISTICS
Adults typically 12–14 in (30.5–35.6 cm) in length. Deep bodied and laterally compressed. Silvery in color, with brassy sides and a dark blue-green back. A row of sharp scutes extends along the ventral edge of the belly. A large dark spot is located behind the gill cover, followed by several smaller spots.

DISTRIBUTION
Western Atlantic from Nova Scotia, Canada, to Indian River, Florida.

HABITAT
Primarily pelagic fish. Found in waters over the continental shelf. Moves inshore to bays, inlets, and estuaries in the summer.

BEHAVIOR
Forms large, compact schools of juveniles and adults. Stratifies by size along the Atlantic seaboard during annual north-south migrations. Fish of all ages congregate near Cape Hatteras, North Carolina, during the winter months. Most adults move northward after March, with the largest fish migrating as far as the Gulf of Maine; some adults move southward as far as to waters off of Florida. Fish of all ages and sizes then return to Cape Hatteras in late autumn. Atlantic menhaden also move in and out of inshore habitats with the tides, the season, and the weather.

FEEDING ECOLOGY AND DIET
Feeds by filtering phytoplankton and zooplankton, including diatoms, copepods, and euphausids.

REPRODUCTIVE BIOLOGY
Spawns in the open ocean throughout the year. Eggs are buoyant and hatch at sea. Over one to three months, larvae are transported to estuaries by ocean currents, where they develop into juveniles. Most Atlantic menhaden first spawn during their third year of life. Females exhibit high fecundity levels, producing about 38,000–50,000 eggs per female.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Previously used by Native Americans and early European colonists as fertilizer. A fishery developed for menhaden during the late 1800s and early 1900s. Today used primarily to produce fish meal and oil, although some are marketed fresh, salted, canned, or smoked. Due to the large biomass represented by this species, menhaden constituted around 30% of commercial fisheries landings along the U.S. Atlantic coast in 2000. ◆

Atlantic herring
Clupea harengus

FAMILY
Clupeidae

TAXONOMY
Clupea harengus Linnaeus, 1758, European seas. This species was previously considered a subspecies, *Clupea harengus harengus*, but recent taxonomic classifications distinguish it as a separate species.

OTHER COMMON NAMES
English: Bank herring, brit, fall herring, hern, herning, herron, labrador herring, mesh herring, murman hering, Norwegian herring, sardine, sea Atlantic herring, sea stick, shore herring, split, spring herring, summer herring, yawling; French: Hareng atlantique, hareng de l'Atlantique; German: Allec, Hering, Silling; Spanish: Arenque, arenque del Atlántico.

PHYSICAL CHARACTERISTICS
Maximum size 17.7 in (45 cm), but most fish captured in fisheries are 11.8–13.8 in (30–35 cm). Elongate and slender. Back is dark blue-green (or bluish green), sides and belly are silvery, and snout is blackish blue. There are no distinct dark spots on the body or fins. The belly is rounded with scutes, but has no prominent keel. The lower jaw of the Atlantic herring is slightly longer than the upper jaw.

DISTRIBUTION
Eastern Atlantic Ocean, from the northern Bay of Biscay northward to Spitzbergen and Novaya Zemlya, and around Iceland and southern Greenland. Also found in the western Atlantic, from southwestern Greenland, around Labrador, and south to South Carolina.

HABITAT
Coastal pelagic species. Found at depths ranging from near the surface down to 656 ft (200 m).

BEHAVIOR
Schools in coastal waters. Exhibits complex feeding and spawning migrations, but the timing and extent of migrations varies by morphological race of the fish. Stays in deep water during the day but moves to the surface at night. Most migrate to coastal spawning grounds at the onset of spawning seasons. Also migrates north and south seasonally to feeding areas and for over wintering.

FEEDING ECOLOGY AND DIET
During their first year of life, Atlantic herring feed on small planktonic copepods. Thereafter, they consume mostly copepods, but also amphipods, mysids, small fishes, and ctenophores. Atlantic herring locate food particles visually, but they can switch to filter feeding if they encounter a high density of small food particles. This species is important as prey in the marine food chain, and it is consumed by larger fishes, squids, skates, whales, and seabirds.

REPRODUCTIVE BIOLOGY
Exhibits a wide range of spawning behaviors and strategies that vary by stock and race. At least one population spawns in any month of the year, but each race spawns at a different time and place. Off Greenland, these fishes spawn in up to 16 ft (5 m) of water; autumn-spawning herrings in the North Sea spawn at depths of 656 ft (200 m). The eggs are adhesive and are laid over rocks, stones, gravel, sand, algae, or vegetation on the seabed. Atlantic herring reach their sexual maturity at three to nine years of age, and females may produce 20,000–40,000 eggs.

CONSERVATION STATUS
Populations fluctuate widely. Some stocks are considered overfished, while others have shown recent increases in abundance. Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The commercial fishery for Atlantic herring ranks among the most important in the world in terms of biomass and value. Atlantic herring were a major item of trade between Scandinavian countries and western European countries as early as the twelfth century. The western Atlantic fishery developed in the 1800s and supplied fish that were sold as bait or sardines. In the United States and Canada, most Atlantic herring are sold as sardines or are converted to fish meal or oil. Smoked, salted, pickled, fresh, and frozen herring are more common in Europe. Herring form an important part of the cuisine of certain cultures; it is particularly central to the Jewish cuisine due to dietary and cooking restrictions observed by many Jews. ◆

Pacific herring
Clupea pallasii

FAMILY
Clupeidae

TAXONOMY
Clupea pallasii Valenciennes, 1847, Kamchatka, Russia. This species was previously considered a subspecies, *Clupea harengus pallasii*, but recent taxonomic classifications distinguish it as a separate species. One subspecies: *Clupea pallasii marisalbi* Berg, 1923.

OTHER COMMON NAMES
English: Herring, North Pacific herring, Oriental herring; French: Hareng du Pacifique, hareng pacifique; German: Pazifischer Hering; Spanish: Arenque del Pacifico.

PHYSICAL CHARACTERISTICS
Maximum size 18 in (46 cm), but most are less than 11.8 in (30 cm). Elongate and slender, with a rounded belly and scutes. Back is dark blue to olive, the sides and belly are silvery. There are no distinct dark spots on the body or fins. Distinguished from the Atlantic herring by having fewer vertebrae and fewer postpelvic scutes.

DISTRIBUTION
Arctic Sea from the White Sea eastward to the Ob Inlet. They range in the Western Pacific along the coast of Russia, south to Japan and Korea. In the eastern Pacific, they are found from the Kent Peninsula and Beaufort Sea, around Alaska, and south to Baja California, Mexico.

HABITAT
Coastal pelagic species that uses estuaries and bays for spawning.

BEHAVIOR
Begins schooling as a juvenile and is found in inshore waters during this life history stage. Adults form schools at sea, but they migrate to inshore waters, including bays and estuaries, to spawn. They migrate from the sea to inshore waters, entering bays and estuaries to spawn. They also migrate daily from deep waters during the day to shallower portions of the water column at night. Pacific herring do not undertake extensive latitudinal migrations along the coast.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, including euphausids, copepods, mysids, and amphipods. Serves as food for a wide variety of predatory fishes and seabirds.

REPRODUCTIVE BIOLOGY
Breeds from December to July, with the precise timing of spawning varying with latitude. Adults congregate near inshore spawning grounds several weeks before spawning. Herring spawn over a variety of substrates, including rocks, algae, vegetation, and flat surfaces. The female deposits rows of eggs along the substrate; the eggs are then fertilized by the males. Spawning occurs several days at a time, with events separated by a day to several weeks. In California, these herring spawn at age two to three, but members of the species that inhabit waters at higher latitudes reach maturity later.

CONSERVATION STATUS
Not listed by the IUCN, but populations are sensitive to shoreline development and fishing pressures.

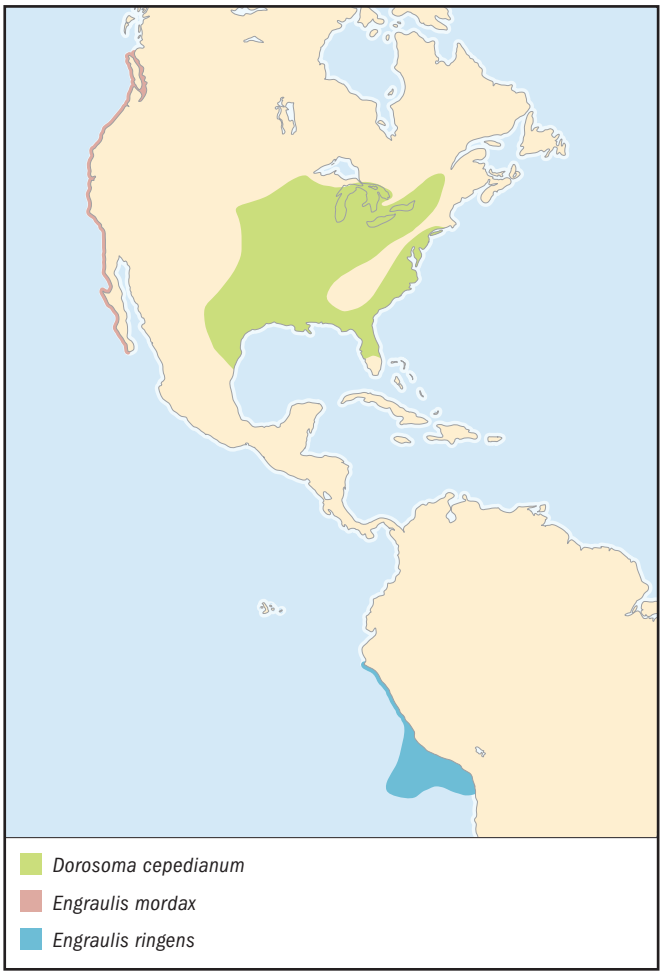
SIGNIFICANCE TO HUMANS
Previously used by Native Americans as fresh or salted food and for bait. In the early 1900s, commercial fisheries developed along the west coast of the United States and Canada for salted and canned herring and for the reduction of the fish to meal and oil. These fishes are valued in Russia as food and are utilized fresh, dried, smoked, canned, and frozen. In the eastern Pacific, the roe and eggs are taken to supply Asian markets. Pacific herring also are used in Chinese medicine. ◆

Gizzard shad
Dorosoma cepedianum

FAMILY
Clupeidae

TAXONOMY
Dorosoma cepedianum Lesueur, 1818, Baltimore, Maryland and Philadelphia, Pennsylvania, United States.

OTHER COMMON NAMES
English: American gizzard shad, eastern gizzard shad, gizzard mud, gizzard nanny shad, hickory shad, mud shad, nanny shad, skipjack winter shad; French: Alose à gésier, alose a gésier américaine, aloser noyer; Spanish: Sábalo molleja.



PHYSICAL CHARACTERISTICS
Maximum size 22.4 in (57 cm). Silver to brassy body with a bluish back and white belly. There is a large dark spot behind the operculum and above the pectoral fin. Snout is rounded and blunt. The last dorsal fin ray extends to a long filament.

DISTRIBUTION
Atlantic coast of the United States from New York, southward into the Gulf of Mexico and to the basin of the Rio Pánuco in Mexico. Found inland in the Great Lakes, St. Lawrence, Mississippi, Atlantic, and Gulf Slope drainages, with its east-west range extending from Quebec to North Dakota in the north and from Florida to New Mexico in the south.

HABITAT
Can tolerate salinities from fresh water to 33 or 34 parts per 1,000, but is most common in freshwater lakes, reservoirs, swamps, and slow-moving rivers. Adults are found in estuaries and protected bays; the young are sometimes found far upstream in small streams.

BEHAVIOR
Forms schools. Individuals may be seen leaping out of the water and skipping along the surface on their sides, giving rise to one common name for the species, the skipjack.

FEEDING ECOLOGY AND DIET
Young gizzard shad feed on zooplankton. As they mature, gizzard shad become herbivorous filter feeders, consuming phytoplankton and algae on the bottom of the water body.

REPRODUCTIVE BIOLOGY
Spawns from late winter through most of the summer; the exact spawning dates relate to latitude and water temperature. Adults spawn near the surface, usually in groups of two males and one female. The eggs, which are very small (0.03 in [0.75 mm] in diameter) sink and adhere to the bottom. They hatch in three days to one week, depending on temperature.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Young gizzard shad are important forage fishes that sustain other game and commercial fish species. In some areas, the abundance of gizzard shad creates a nuisance for humans when low temperatures, low oxygen, or disease trigger the death of a large number of fish that often wash onto shores and decay. Gizzard shad also create problems for fisheries; they entangle the nets of commercial fishermen and out-compete many preferred recreational species. The gizzard shad is used for fertilizer and as a component of cattle and hog food. ◆

European pilchard
Sardina pilchardus

FAMILY
Clupeidae

TAXONOMY
Sardina pilchardus Walbaum, 1792, Cornwall, England.

OTHER COMMON NAMES
English: Pilchard, sardine, true sardine; French: Sardine, sardine commune, sardine d'Europe; German: Pilchard, Sardine; Spanish: Majuga, parrocha, sardina, sardiña, xouba.

PHYSICAL CHARACTERISTICS
Can attain lengths of 9.8 in (25 cm). Body elongate with a rounded belly that has scutes but not a defined keel. Back dark green or olive in color, with golden flanks and a silvery white belly. There is a series of dark spots along the upper flanks.

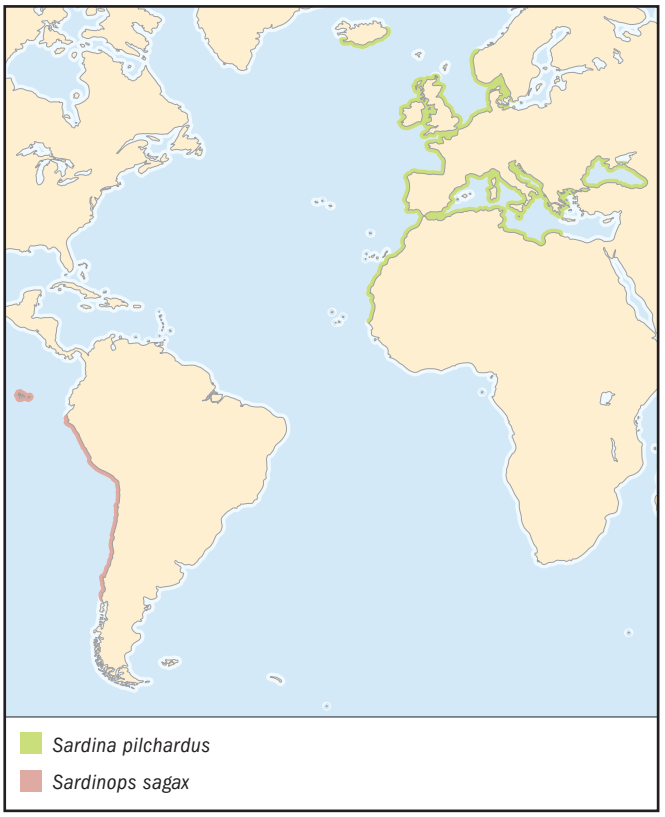
DISTRIBUTION
Northeast Atlantic from Iceland and the North Sea south to Senegal. Also found in the western Mediterranean and Adriatic Seas.

HABITAT
Coastal, pelagic species that is found at water depths of 82–180 ft (25–55 m) during the day and 49–115 ft (15–35 m) at night.

BEHAVIOR
Forms schools and undertakes diel migrations in the water column, staying at deeper depths during the day and rising to shallower waters at night.

FEEDING ECOLOGY AND DIET
Feeds mainly on planktonic crustaceans, but may also consume larger planktonic organisms.

REPRODUCTIVE BIOLOGY
Breeds at 66–82 ft (20–25 m) depth up to 62 mi (100 km) offshore. Spawning time varies by geographic location, taking place in April in the English Channel, from June to August in the North Sea, from September to May along European coasts in the Mediterranean, and from November to June along



African coasts in the Mediterranean. The eggs are buoyant and develop in the water column.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Constitutes an important fishery throughout its range. Catches have steadily risen since 1950, and in 1999, over 900,000 tons (816,466 tonnes) was harvested. The fish is marketed fresh, frozen or canned but may also be utilized in dried or smoked forms. ◆

South American pilchard
Sardinops sagax

FAMILY
Clupeidae

TAXONOMY
Sardinops sagax Jenyns, 1842, Lima, Peru.

OTHER COMMON NAMES
English: Chilean pilchard, Chilean sardine, Pacific American sardine, pilchard, sardina, sardine; French: Hareng, Pilchard sudaméricain, Sardinops du Chili; German: Chilenishe Sardine, Südeamerikanische Sardine; Spanish: Pilchard chileña, Sardina, Sardina española.

PHYSICAL CHARACTERISTICS
May grow to 12 in (30 cm), but sizes of 8 in (20 cm) are more common. Bluish on the back and silvery on the sides. Round-bodied and has a keel with scutes along the belly.

DISTRIBUTION
Eastern Pacific along the coasts of Peru and Chile; also found near the Galápagos Islands.

HABITAT
Coastal, pelagic species that is found to depths of around 131 ft (40 m).

BEHAVIOR
Forms large schools and migrates up and down in the water column on a diel cycle.

FEEDING ECOLOGY AND DIET
Feeds mainly on planktonic crustaceans but may also consume phytolankton. Bethnic organisms, including ostracods and polychaete worms make up a minor portion of the diet of adults.

REPRODUCTIVE BIOLOGY
Spawns twice each year by broadcasting eggs. Eggs and larvae are pelagic and develop in the water column.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Forms the basis of a substantial fishery off Peru and Chile. The fishery reached a peak of 6.5 million tons (5.9 million tonnes) in 1985, corresponding to the crash of the Peruvian anchoveta fishery caused by El Niño. However, catches have declined since then, and the total harvest in 1999 was less than 450,000 tons (408,233 tonnes). ◆

Bay anchovy
Anchoa mitchilli

FAMILY
Engraulidae

TAXONOMY
Anchoa mitchilli Valenciennes, 1848, New York, United States.

OTHER COMMON NAMES
English: Common anchovy; French: Anchois américain; Spanish: Anchoa de caleta.

PHYSICAL CHARACTERISTICS
Small species, typically 3–4 in (7.6–10.2 cm) total length. Nearly transparent and greenish in color, with a silvery band along the side of the body. Snout overhangs the mouth and low jawbone extends well beyond the eye.

DISTRIBUTION
Atlantic coast of North America from Casco Bay, Maine, to the Florida Keys, and westward around the Gulf of Mexico south to the Yucatán peninsula.

HABITAT
Primarily an estuarine and inshore coastal species. Utilizes a wide variety of habitats including bays, sandy beaches, marshes, islands, and spoil banks. Typically found over muddy bottoms or in vegetation. Tolerates a wide range of salinities but is often found in brackish water.

BEHAVIOR
Swims in schools. Migrates seasonally from deep waters in winter to shallow shores and wetlands in summer.

FEEDING ECOLOGY AND DIET
Plankton feeder; primarily consumes mysids and copepods. Small fishes, gastropods, and isopods are occasionally taken.

REPRODUCTIVE BIOLOGY
Spawns from late winter to early fall when water temperatures are around 68°F (20°C). Spawning takes place during the evening hours in shallow waters near barrier islands, in bays, and in estuaries. Spawning usually occurs in large schools. Females broadcast eggs, which are fertilized in the water column by males. Eggs float near the water surface for approximately 24 hours after fertilization before they hatch. Bay anchovies mature to adults in two and one-half months.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Used as bait and to make anchovy paste. Important as forage fishes in food chains that sustain other commercial and recreational fishery species in estuaries and coastal areas. ◆

Northern anchovy
Engraulis mordax

FAMILY
Engraulidae

TAXONOMY
Engraulis mordax Girard, 1854, San Francisco, California, United States.

OTHER COMMON NAMES
English: Anchovy, Californian anchovy, North Pacific anchovy, pinhead; French: Anchois de California, anchois du nord, anchois du Pacifique, anchois du Pacifique nord; German: Amerikanische Nordpazifische, Amerikanische Sardelle; Spanish: Anchoa de California, anchoa del Pacifico, anchoveta, anchoveta de California, anchoveta norteña.

PHYSICAL CHARACTERISTICS
Grows to 4 in (10 cm). Body slender and elongate but round in cross section. Back is green and sides are silvery, including a stripe along the flank in young individuals. Large head and mouth with a pointed snout.

DISTRIBUTION
Northern Pacific from Vancouver Island, Canada, to Baja California, Mexico.

HABITAT
Pelagic marine species found to depths of 984 ft (300 m). Usually stays in coastal waters within 18.6 mi (30 km) of shore but may range as far as 298 mi (480 km) offshore. Enters estuaries, bays, and inlets during the spring and summer.

BEHAVIOR
Forms schools during most of the year, although these become smaller or break up in late spring, typically around the end of spawning in April or May. Moves to inshore waters during spring and summer and migrates offshore in the fall and winter. Diel migrations also occur, with the northern anchovy remaining at depths during the day and approaching the surface in low-density schools at night.

FEEDING ECOLOGY AND DIET
Obtains food both by filter feeding and particulate biting. Feeds on plankton, primarily euphausids, copepods, and decapod larvae. Northern anchovies are an important forage species for other fishes, birds, and marine mammals.

REPRODUCTIVE BIOLOGY
Spawns in inlets and offshore, with spawning activity occurring at night. Two major spawning areas exist in coastal waters off southern California and Baja California, Mexico. Eggs are broadcast and fertilized in the water column, then float and incubate for two to four days before hatching. Spawning takes place throughout the year, and individual females may spawn several times each year. However, as a whole, the species exhibits a clear peak in spawning during the winter and early spring.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Supports a commercial and bait fishery, which developed after the collapse of the Pacific sardine fishery in the 1940s. Approximately 25 million pounds were landed in 2000, with most used for fish meal, fertilizer, and animal feed. A small portion is consumed by humans in pickled or salted forms. ◆

Anchoveta
Engraulis ringens

FAMILY
Engraulidae

TAXONOMY
Engraulis ringens Jenyns, 1842, Iquique, Chile.

OTHER COMMON NAMES
English: Anchovy, Peruvian anchoveta; French: Anchois du pérou, anchois péruvien; German: Perusardelle, Südamerikanische Sardelle; Spanish: Anchoa, anchoa bocona, anchoveta, anchoveta peruana, atunera, chicora, manchuma, manchumilla, peladilla, sardina bocona.

PHYSICAL CHARACTERISTICS
Grows to 7 in (18 cm) and has a slender, elongated body that is round in cross section. Its large snout and mouth are similar to those of other anchovies. Silvery in color; juveniles have a stripe along the flank.

DISTRIBUTION
West coast of South America along the Peru Current, typically from around Aguja Point, Peru, south to Chiloë, Chile.

HABITAT
Pelagic species. Occurs in surface waters, usually within 49 mi (80 km) of the shore, but occasionally offshore to 99 mi (160 km).

BEHAVIOR
Forms huge schools. Descends to deeper waters during the day but rises to the surface at night.

FEEDING ECOLOGY AND DIET
Filter feeder. Depends entirely on the plankton of the Peru Current for food. Diet consists largely of diatoms, which make up as much as 98% of its consumption according to some studies. It also consumes copepods, euphausids, fish eggs, and dinoflagellates. Seabirds prey heavily on schools of anchoveta.

REPRODUCTIVE BIOLOGY

Matures at around one year of age. Breeds throughout the year, but two peaks of spawning occur in late winter and early autumn. Their buoyant ellipsoidal eggs are broadcast into the water column and fertilized.

CONSERVATION STATUS

Not listed by the IUCN, but populations vary greatly with climatic conditions. El Niño, the oceanographic condition that results in warmer water in the Pacific Ocean, slows and may stop the upwelling of nutrient rich waters in the Peru Current. This can have devastating effects on the anchoveta by dramatically reducing its planktonic food base.

SIGNIFICANCE TO HUMANS

Previously the world's largest fishery in terms of biomass in 1971, with over 13 million tons (11.7 million tonnes) harvested. Populations declined during the 1970s and 1980s due to overfishing and the occurrence of severe El Niño events in 1972–1973 and 1982–1983. Since that time, anchoveta populations have recovered and the species again constitutes a major fishery. In 2000 the anchoveta comprised over 12 million tons (11 million tonnes) of a total harvest in the southeastern Pacific of around 16.5 million tons (15 million tonnes) for all fishes. Peru and Chile rely upon this fishery as a major export and source of income. It is utilized primarily as fish meal and oil.

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Organizations

Menhaden Resource Council. 1901 N. Fort Myer Drive, Suite 700, Arlington, VA 22209 USA. Phone: (703) 796-1793. E-mail: resource@menhaden.org Web site: <http://www.menhaden.org>

Other

FAO Fisheries Department. (13 Nov. 2002) <http://www.fao.org/fi/default.asp>

FishBase. 8 Aug. 2002 (13 Nov. 2002). <http://www.fishbase.org/search.cfm>

Katherine E. Mills, MS

Gonorynchiformes
(Milkfish and relatives)

Class Actinopterygii
Order Gonorynchiformes
Number of families 3

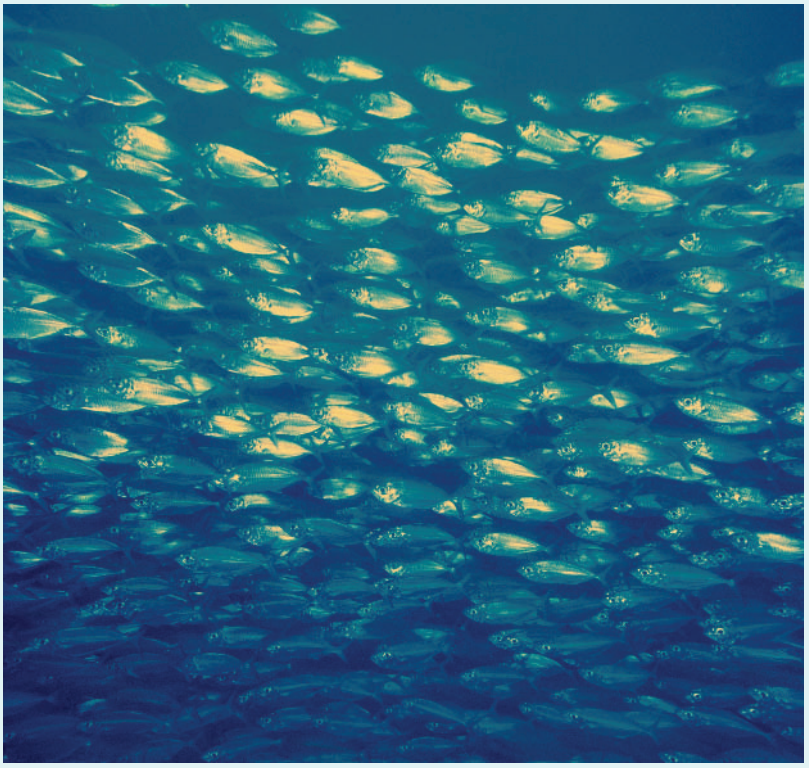


Photo: School of milkfish (*Chanos chanos*) in the warm waters along the continental shelves and around islands in the Indo-Pacific. (Photo by Stuart Westmorland/Corbis. Reproduced by permission.)

Evolution and systematics

The placement of the order Gonorynchiformes within Actinopterygii (the bony fishes) has been problematic at best. This may have been due to the enormous amount of morphological variation among gonorynchiform subgroups. For example, individuals in the genus *Phractolaemus* are facultative air breathers and show many morphological specializations of the head, while members of genera *Cromeria* and *Grasseichthys* are paedomorphic, and show extreme cranial miniaturization. As a result, few researchers could believe that these genera could belong to the same taxonomic group. Pivotal studies by Rosen and Greenwood in 1970 and Fink and Fink in 1981, however, demonstrated that the Gonorynchiformes do form an evolutionary assemblage and belong to the superorder Ostariophysi, as the sister-group to those fishes with a functioning Weberian apparatus (e.g., carps, minnows, and catfishes). In the studies of Gayet in 1993 and Grande and Poyato-Ariza in 1999, the taxonomic composition and evolutionary relationships within this unusual group of fishes was investigated. These researchers corroborated previous studies in the placement of Gonorynchiformes within Ostariophysi, and Grande and Poyato-Ariza divided the group into three families: Chanidae, Gonorynchidae, and Kneriidae. Characteristics identifying gonorynchiform fishes include a unique arrangement of intermuscular bones, as well as a specialized articulation between the first neural arch of the vertebral column and the back of the skull.

The Gonorynchiformes is an ancient group, with a fossil record dating back to the early Cretaceous period (about 100 million years ago). Although controversial, the habitats, or paleoecologies, of the fossil forms were most likely subtropical. This is indicated by the plants and animals collected in these deposits, whose living relatives have subtropical habitats today. Because many fossil gonorynchiforms are endemic to specific geographic localities, an understanding of their distribution patterns can provide insight into the early history of Earth. For example, well-preserved fossil chanids have been collected from the Santana Formation of eastern Brazil and the bituminous shales of Equatorial Guinea, supporting a hypothesized physical connection between the continents of South America and Africa. This connection may have lasted until the early Tertiary period. Additional chanid fossils have been collected from marine and lacustrine deposits of Germany and Spain, while fossils belonging to the family Gonorynchidae have been found in early Cretaceous marine deposits of Israel and Lebanon and from freshwater deposits of North America. This interesting fossil-distribution pattern has lead researchers (such as Jerzmanska in 1977 and Gaudant in 1993) to hypothesize a possible Tethys Sea (an ancient sea that once separated northern Africa from Asia) origin for the Gonorynchiformes, with subsequent dispersal routes throughout the Pacific Ocean. This model, however, does not discount the possible Pangaean origin of the group as proposed by Patterson in 1975.

As of 1999, 20 nominal gonorynchiform genera (7 living and 13 fossil) and about 50 species had been described. These genera are grouped into three families. The first, the Chanidae, consists of one living representative, *Chanos chanos*, and five extinct forms. Chanids have similar body shapes and are identifiable by a distinctively shaped permaxilla, a notch in the anterior border of the dentary, and an anteroventral process of the hyomandibular, a bone that connects the jaws to the cranium. The second family, the Gonorynchidae, is represented by the marine Indo-Pacific form *Gonorynchus*, its extinct sister group *Notogoneus*, and four Cretaceous marine groups from the Middle East. These share multiple fusions of the caudal fin skeleton; there exists a fusion of hypurals 1 and 2, as well as the parhypural with preural centrum 1. In addition, all gonorynchids have a patch of conical teeth on the gill arches, indicating that they can crush and presumably eat crustaceans and organisms with hard shells and carapaces. The third family, the Kneriidae, consists of an interesting assemblage of morphologically diverse fishes: *Phractolaemus*, which breathes atmospheric air; *Kneria*, which sports an elaborate opercular structure on the side of its body that is used as an adhesive device; and *Cromeria* and *Grasseichthys*, two miniature paedomorphs thought at one time to be juveniles. All kneriids are endemic to Africa, they live in freshwater streams and rivers and have no known fossil record. They are grouped taxonomically by distinctive modifications of the back of the skull and anterior neural arches.

Physical characteristics

The Gonorynchiformes is a morphologically diverse assemblage of fishes, ranging in body shape from the silvery herringlike chanids, to the long and slender eel-like gonorynchids, to the tiny minnowlike kneriids. The fishes also vary in size. *Gonorynchus* is one of the larger genera, and can achieve a standard length of over 19.7 in (50 cm), while the miniature *Grasseichthys* achieves an adult body length of a mere 0.71 in (1.8 cm). With the exception of *Kneria*, no sexual dimorphism is evident. In this species, however, males sport a predominant an opercular apparatus, a suckerlike structure. This feature, although present in females, is rudimentary. Its apparent sexually dimorphic occurrence in males has led researchers to assume that its central role is in reproduction. It seems clear that this structure is an adhesive devise and that males can attach themselves to females. Males can also attach themselves to rocks or substrate if necessary.

Distribution

Gonorynchiforms exhibit a widespread geographic distribution, with representatives found on virtually all continents except Antarctica. The milkfish (*Chanos chanos*) and species within the genus *Gonorynchus* inhabit waters of the Indian and Pacific Oceans. Unlike *Chanos* and *Gonorynchus*, fossil representatives are known from separate localities. Fossil chanids, for example, are restricted to Brazil, western Africa, and Europe. Fossil gonorynchids have a more complex distribution, with several members restricted to marine Cretaceous deposits of Lebanon and Israel, whereas *Notogoneus* is found in freshwater deposits of Europe, North America, Mexico, Asia, and Australia. The freshwater kneriids are restricted to specific river systems surrounding the Gulf of Guinea, and the central and southern parts of the Africa. Species of the genera *Kneria* and *Parakneria* are the most geographically widespread, with ranges overlapping throughout Zaire, Angola, Tanzania, Zambia, and the Congo Basin. The species *Kneria auriculata* reaches the southern tip of South Africa. *Phractolaemus* is found in the Niger and Congo River tributaries, whereas *Grasseichthys* is known from streams deep in the forests of Gabon and central Congo. *Cromeria*, the sister species to *Grasseichthys*, is found in tributaries and sandy river banks of the Nile and Niger Rivers.

Habitat

Gonorynchiform species inhabit both marine and freshwater systems. As adults, milkfishes live in marine open-water habitats of the Indian and Pacific Oceans. The milkfish's diadromous nature enables it to breed in inshore waters, where it produces pelagic eggs. When the larvae reach about 0.4 in (1 cm), they enter brackish pools and creeks that have limited contact with the ocean. As mature fishes they return to the sea.

Gonorynchus species often live in coastal sandy habitats. They are nocturnal and remain buried in the sand during the day, thus their common name of sandfishes. Morphologically these fishes are well adapted for living in very dark, open, deep water on the continental shelf. They have a modified lateral line system that extends posterior to the hypural plate, and large eyes that are covered by transparent skin. Sandfishes have been recorded down to a depth of 525 ft (160 m) off Tasmania, and at depths of 340–2,225 ft (104–678 m) on the Chatham Rise and Challenger Plateau off New Zealand. *Gonorynchus* species are thought to breed in deep water. The young are transparent and have a long pelagic postlarval stage. Not until the fish reach a standard length of about 3.5 in (9 cm) do they become benthic. This long pelagic stage in their life cycle allows for the wide dispersal of juveniles.

Little is known about the habitat and ecology of the African kneriids. *Phractolaemus* is thought to inhabit quiet, shaded waters and to be an epiphytic feeder. It also has a gas bladder that is divided into many alveoli, enabling it to breathe atmospheric air. Like *Gonorynchus*, *Cromeria* is found near sandy riverbanks and apparently spends much of its time buried in the sand. The habitat of *Cromeria* is quite different from that of *Grasseichthys*, in that it is found further north in more arid environments. *Grasseichthys* inhabits forested areas farther south.

Behavior

Chanos is a schooling species, both as a juvenile and as an adult. Collection data for *Gonorynchus*, however, suggests that this species is solitary. A solitary behavior is also inferred from collection data for *Phractolaemus*.

Feeding ecology and diet

Feeding ecology seems to be variable, in that only the gonorynchids have teeth and are known to eat crustaceans. *Chanos*, like *Phractolaemus*, has a well-developed epibranchial organ and consumes planktonic prey, most often plant material.

Reproductive biology

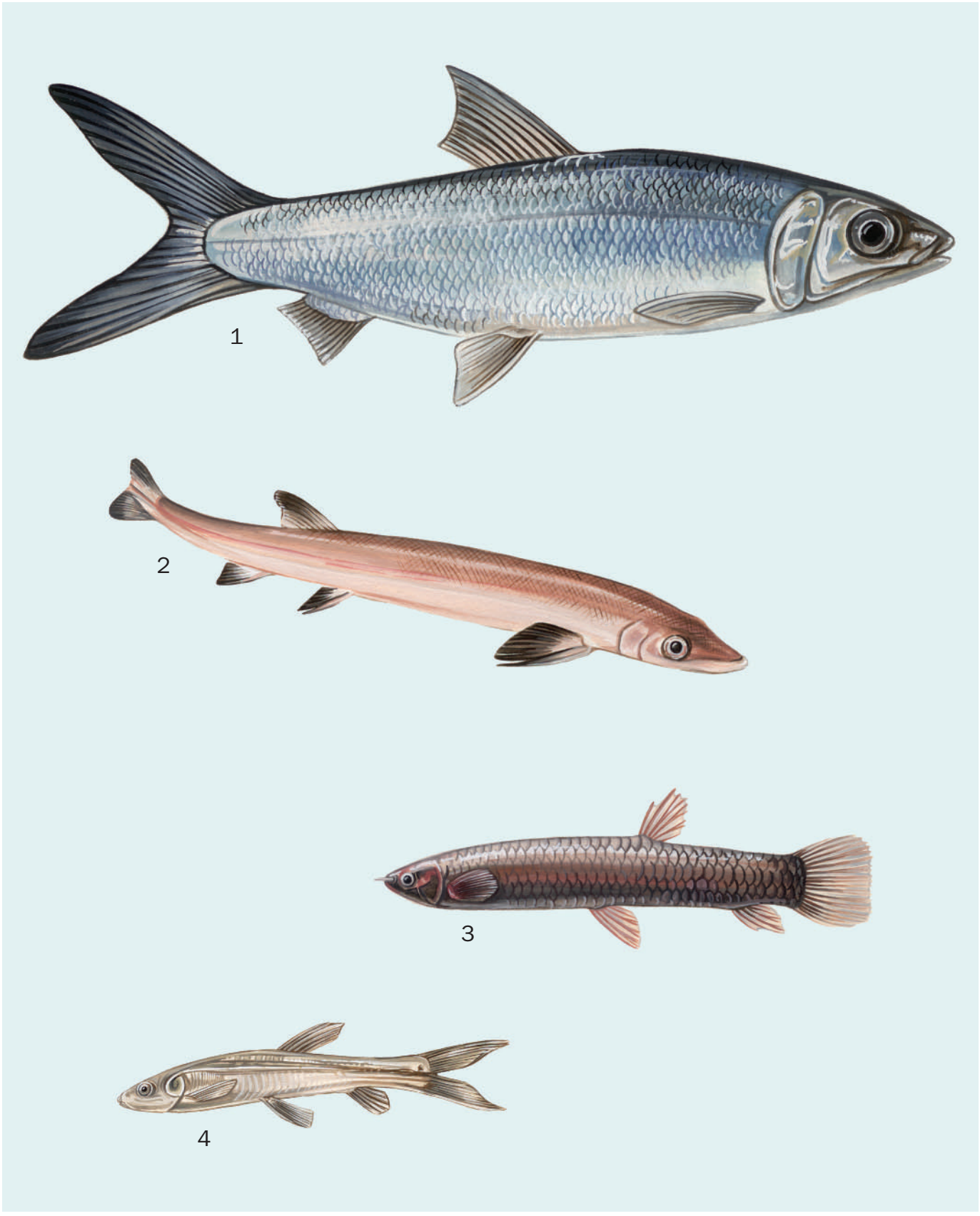
All gonorynchiform species are oviparous, i.e., fertilization and hatching of eggs occurs outside the body. A variety of egg types exists. *Chanos* and *Gonorynchus* produce pelagic eggs, whereas *Kneria* is thought to produce demersal eggs. Sexual dimorphism is clearly evident in *Kneria* and *Phractolaemus*. In all *Kneria* species, adult males develop a characteristic opercular apparatus on the side of the head. Male fishes have been observed swimming attached to females during courtship and mating. By doing this, the male is in close proximity to the female during egg production. In *Phractolaemus*, large thickened keratinized breeding tubercles form on the head and along the sides of adult males. Although the presence of breeding tubercles is characteristic of ostariophysans, tubercules are particularly well developed in *Phractolaemus*.

Conservation status

No gonorynchiform species is listed by the IUCN. However, the South African government has designated at least one *Kneria* species as endangered, and the specialized requirements and extremely limited ranges of other species of *Kneria* and *Parakneria* render them vulnerable to the degradation of their habitats by humans.

Significance to humans

The milkfish is commercially farmed in Southeast Asia. These fishes feature in an extensive aquiculture industry in the Philippines and in Indonesia, where the young are caught close to shore and then reared in coastal ponds. The milkfish is also the subject of a targeted fishery throughout its extensive range.



1. Milkfish (*Chanos chanos*); 2. Sandfish (*Gonorynchus gonorynchus*); 3. African mudfish (*Phractolaemus ansorgii*); 4. *Kneria wittei*. (Illustration by Patricia Ferrer)

Species accounts

Milkfish
Chanos chanos

FAMILY
Chanidae

TAXONOMY
Chanos chanos Forsskål, 1775, Red Sea.

OTHER COMMON NAMES
English: Bangos; French: Chanos; German: Milchfisch; Spanish: Chano, sabalote.

PHYSICAL CHARACTERISTICS
Standard length of over 70.9 in (180 cm). Adults are silvery herringlike fishes with a forked tail, large eyes, pointed snout with terminal mouth, cycloid scales, and an epibranchial organ. The mouth is small and terminal. The jaws are toothless. The dorsal fin has 13–17 rays; the anal fin has 6–8; the pectoral fins 15–17, and the pelvic fins 10–11. Four or five branchiostegal rays are present on each side.

DISTRIBUTION
Throughout the Indian and Pacific Oceans.

HABITAT
Diadromous; adults occur in marine open waters, larvae inhabit brackish inland ponds.

BEHAVIOR
Schooling fishes, both as juveniles and adults.

FEEDING ECOLOGY AND DIET
Larvae in coastal ponds consume diatoms and copepods. Adults have well-developed epibranchial organ used as an extension of the alimentary canal and may live on plant material.

REPRODUCTIVE BIOLOGY
Breeds in inshore waters and produces pelagic eggs. Larvae of about 0.4 in (1 cm) enter brackish waters and as young adults return to the sea.

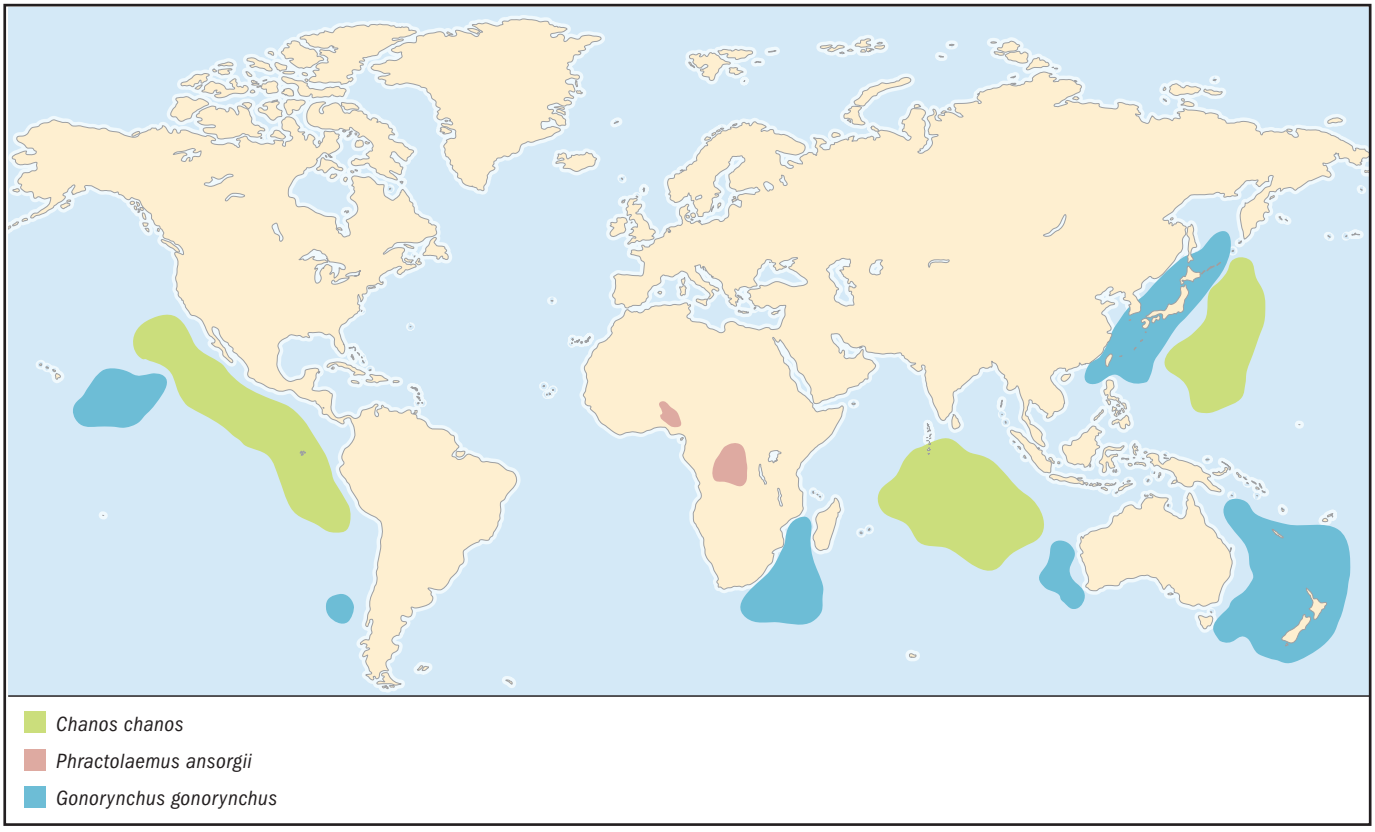
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Commercially raised for food in the Philippines and Indonesia and fished extensively throughout its range. Local fishermen use cormorants with rings around the birds' necks to fish for milkfish. The rings prevent the birds from fully swallowing the fish.◆

Sandfish
Gonorynchus gonorynchus

FAMILY
Gonorynchidae

TAXONOMY
Gonorynchus gonorynchus Linnaeus, 1766, Cape of Good Hope, South Africa.



OTHER COMMON NAMES
English: Beaked sandfish, mousefish, sand eel; French: Caduchon; Spanish: Caduchón; Afrikaans: Spitsbek-sandvis.

PHYSICAL CHARACTERISTICS
Standard length 23.6 in (60 cm). Long slender fishes; mouth inferior, dorsal fin positioned posteriorly (predorsal length at least 70% that of standard length), swim bladder absent, lateral line extends to tip of caudal fin rays, number of lateral line scales ranges from 200–220, presence of median sensory barbel on ventral side of snout, presence of a clover-shaped barbel within the mouth extending from its roof, presence of ctenoid scales that cover the entire body. The young are transparent. Uniformly brown in color, with black patches at the tips of fins.

DISTRIBUTION
Indian and Pacific Oceans.

HABITAT
Marine environments, coastal sandy habitats as well as benthic waters, can reach over 1,970 ft (600 m) in depth.

BEHAVIOR
Does not school. Young have long pelagic postlarval stage that may allow for a wide dispersal of juveniles. Nocturnal, and can be found buried in sand or mud during the day.

FEEDING ECOLOGY AND DIET
A benthic feeder of small decopod crustaceans.

REPRODUCTIVE BIOLOGY
Breeds in deep water. Young are pelagic, subadults of about 3.5 in (9 cm) become benthic.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Kneria wittei

FAMILY
Kneriidae

TAXONOMY
Kneria wittei Poll, 1944, Congo River basin.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Standard length 3.4 in (8.6 cm). Small minnowlike fish. Males have large opercular apparatus, females have rudimentary opercular apparatus. There is a modification and expansion of the epicentral intermuscular bones in both sexes, cycloid scales, tail forked, and mouth terminal. The color pattern is darker on top, lighter on bottom, with darker stripe along side.

DISTRIBUTION
Rivers and tributaries throughout Zaire, Angola, Tanzania, Zambia (i.e., central and southern Africa).

HABITAT
Quiet pools, but most often fast-moving streams with waterfalls.

BEHAVIOR
Schooling fishes, at least during mating periods.

FEEDING ECOLOGY AND DIET
Feeds mostly on algae and plant material. Like most gonorynchiforms, has an epibranchial organ which enables it to filter particulate matter from the water column.

REPRODUCTIVE BIOLOGY
Males attach themselves to females via the opercular apparatus during courtship, ensuring that the largest number of demersal eggs laid by the female will be fertilized.

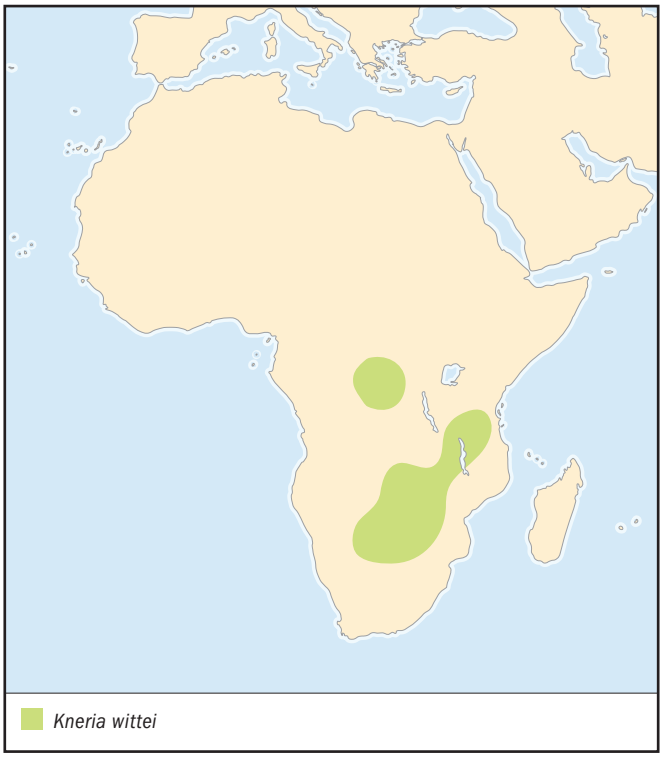
CONSERVATION STATUS
Not listed by the IUCN. However, like all freshwater African gonorynchiforms, habitat destruction may eventually result in an endangered status.

SIGNIFICANCE TO HUMANS
None known. ◆

African mudfish
Phractolaemus ansorgii

FAMILY
Kneriidae

TAXONOMY
Phractolaemus ansorgei Boulenger, 1901, Niger delta. Species of the genus *Phractolaemus* have traditionally been placed within their own family, Phractolaemidae, but according to current research, they are closely related to kneriids and have been placed in Kneriidae by Grande and Poyato-Ariza.



OTHER COMMON NAMES
English: Hingemouth, snake mudhead; German: Afrikanischer Schlammfisch.

PHYSICAL CHARACTERISTICS
Standard length 6 in (15 cm). Elongate, cylindrical body with large cycloid scales. Head is small, broad, and strongly ossified; eyes are small and laterally positioned. Infraorbital bones two, three, and four are greatly enlarged. The mouth is highly projectile and capable of being thrust forward; at rest the mouth folds over into a depression on the upper surface of the snout. The mouth has no teeth except for a conical tooth on each dentry near the symphysis. There is a single narial opening preceded by a barbel. The opercular openings are narrow due to a sealing of the opercular boarder to the body wall. The interopercle is spinelike, and the preopercles are greatly enlarged, overlapping along the ventral midline of the body. There are six pelvic fin rays, six dorsal rays, and six anal fin rays. Three slender branchiostegal rays are evident. Unlike other gonorynchiform fishes, the swim bladder is divided into alveoli, which enables the fish to breathe atmospheric air. Body is uniformly gray above, light brown on the sides, pale ventrally with darkly colored fins.

DISTRIBUTION
Tropical Africa ranging through the lower Niger drainage and central Zaire basin.

HABITAT
Quiet, low-oxygenated muddy waters.

BEHAVIOR
Little is known about the behavior of this species. Unlike other gonorynchiforms, it is able to breathe atmospheric air, an ability that has made this fish of interest to aquarists.

FEEDING ECOLOGY AND DIET
Feeds on small, mud-dwelling organisms. Based on the presence of a moderately developed epibranchial organ, some researchers believe this species is an epiphytic feeder.

REPRODUCTIVE BIOLOGY
Utilizes external fertilization. Exhibits clear sexual dimorphism, as males sport conspicuous whitish breeding tubercles on the head, along the lateral line, and on the caudal peduncle.

CONSERVATION STATUS
Not listed by the IUCN. However, continued habitat destruction will undoubtedly affect the population dynamics and future of this fish.

SIGNIFICANCE TO HUMANS
Not an economically important food fish, but has been imported into the United States as an aquarium fish.

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Terry Grande, PhD

Cypriniformes I
(Minnows and carps)

Class Actinopterygii
Order Cypriniformes
Number of families 1 of minnows and carps

Photo: Roach (*Rutilus rutilus*), a freshwater fish of Europe. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Cypriniforms are typical freshwater fishes in which the upper jaw is usually protractile; the mouth (jaws and palate) is always toothless; the adipose fin is absent; the head almost always scaleless; and barbels are either present or absent. These fishes have Weberian ossicles (four small bones and their ligaments connecting the swim bladder to the inner ear for sound transmission). The fifth ceratobranchial is enlarged as the pharyngeal bone, with teeth ankylosed (joined) to it. For cyprinids, pharyngeal teeth are in one to three rows, and there are never more than eight teeth in any one row; for non-cyprinid cypriniforms, pharyngeal teeth are usually greater in number but only in one row.

Generally, Cypriniformes is divided into two monophyletic groups: the family Cyprinidae and the non-cyprinid cypriniforms. The Cyprinidae includes different kinds of minnows and carps. The non-cyprinid cypriniforms are composed of the family Catostomidae (suckers), family Gyrinocheilidae (algae eaters), and many different loaches. The relationships among the non-cyprinid cypriniforms are still in debate. Recent molecular data suggest that suckers could be at the basal position of this group, followed by the algae eaters and then the different loaches. This chapter focuses on the family Cyprinidae.

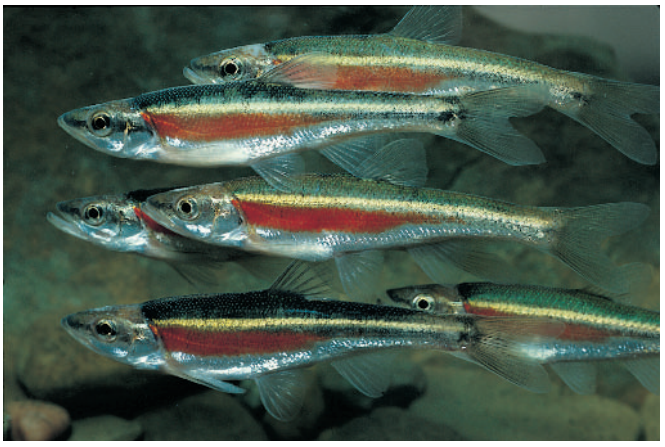
The recognition and composition of the subfamilies in the Cyprinidae is still in question. Several proposals have been provided based on morphological characters, and the recent molecular data support a combination of them. Thus, 9 subfamilies, forming two phyletic lineages, are recognized. The first lineage consists of subfamilies Cyprininae, Barbinae (including Schizothoracinae), and Labeoninae. The second lineage consists of subfamilies Rasborinae (Danioninae), Leuciscinae, Tincinae, Acheilognathinae, Gobioninae (including Gobiobotinae), and Xenocyprinae (the east Asian group, including Cultrinae, Hypophthalmichthyinae, etc.). All these different subfamilies could have evolved from *barbus*-like cyprinids, with parallel evolutions of certain characters, such as the loss of three-rowed pharyngeal teeth, loss of barbels, and so on.

The earliest cyprinid fossils are known from South China from the Eocene period, and could represent cyprinini and rasborini; the earliest European and North American ones are of Oligocene age. The cyprinids might have originated in Asia and dispersed to North America through the Bering land bridge and to Europe before the upheaval of the Tibetan Plateau. The earliest record of cyprinids in Africa was in the Miocene period. Cyprinids may have migrated from Southeast Asia to Africa through the Near East during the Miocene.

Physical characteristics

Normally, carps are fusiform or streamlined, with the body somewhat compressed. The dorsal fin is long (in *Cyprinus*) or short, and the last unbranched fin ray is soft, hard, or spine-like, with serrations on the posterior edge in Cyprininae and some barbinins. Pectoral fins and ventral fins are in the normal position. The anal fin has five soft, branched fin rays in Cyprininae, Barbinae, and Labeoninae species; six in Gobioninae species; and seven or more in other groups. The last unbranched anal fin ray is soft, hard, or spine-like. The caudal fin is forked in all species.

Breams and some cultrin species have a very deep body, which may protect them from predators' bites. Living on the river bottom and adapted to fast running water, most Gobionine species have a round and slender body and are called "stick fish" by fisherman. The head of *Luciobrama* is strongly elongated, forming a pipe shape.



Redside dace (*Clinostomus elongatus*) swimming in Ohio. (Photo by Gary Maeszaros/Photo Researchers, Inc. Reproduced by permission.)

A northern pikeminnow (*Ptychocheilus oregonensis*) resting on the rocks of the Middle Fork Boise River in Idaho, USA. (Photo by William H. Mullins/Photo Researchers, Inc. Reproduced by permission.)

Most carps and minnows are covered with scales. However, the leather carp, one variation of the common carp, has no scales. Some Schizothoracin fishes are half or completely naked. The sawbwa barb, *Sawbwa resplendens*, which is endemic to Lake Inle in Myanmar, is completely naked and a little transparent. The lateral line is complete in most species but incomplete in some small fishes, such as *Aphyocypris* and *Rhodeus*.

The most common coloration for carps is dark green on the back and whitish on the belly, which makes the fishes difficult to spot both from above the water and under the water. However, color variations are also very common. Some *gobio* species have different dots; *Danio* and *Zacco* species have beautiful stripes; and some barbin species and bitterlings are even more colorful.

The largest species are the tetraploid barbine *Catlocarpio siamensis* of Thailand, which is known to reach at least 8.2 ft (2.5 m) and probably 9.84 ft (3 m), and *Tor putitora* of the Brahmaputra River (eastern India), which reaches about 8.86 ft (2.7 m); in North America the Colorado pikeminnow, *Ptychocheilus lucius*, can reach 5.9 ft (1.8 m); other large Asian species (6.6 ft [2 m] or larger) include *Elopichthys bambusa* and *Barbus esocinus*. The smallest cyprinid is *Danionella translucida*, distributed in Burma, in which females are mature at about 0.4–0.43 in (10–11 mm) and the longest specimen known is 0.47 in (12 mm).

Distribution

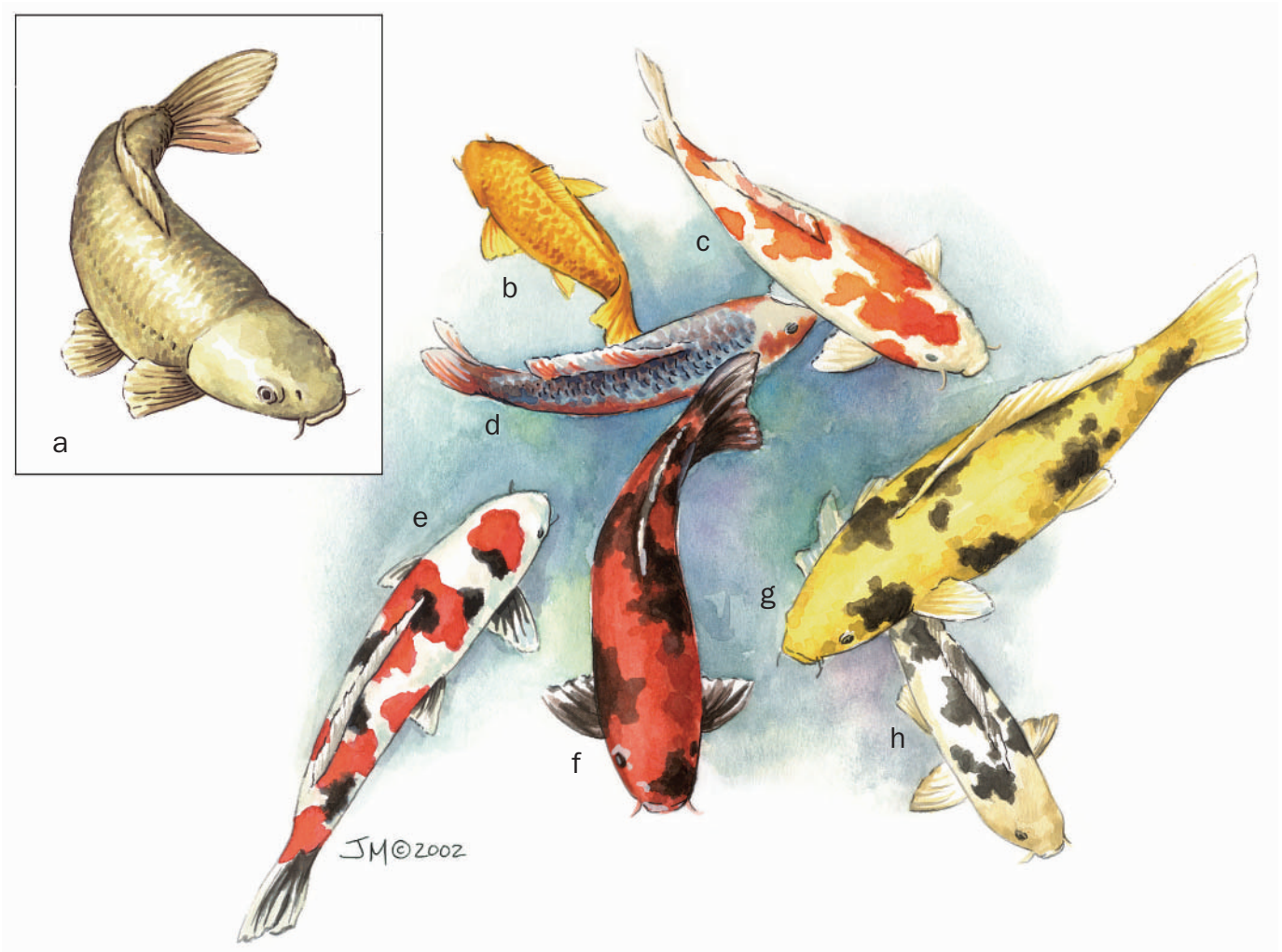
Cyprinidae is the largest family of freshwater fishes, with about 210 genera and about 2,010 species. Of this figure, about 1,270 species are native to Eurasia (the greatest generic diversity and number of species is in China and Southeast Asia; China alone contains about 532 species in 132 genera); about 475 species in 23 genera are native to Africa; and about 270 species in 50 genera are native to North America. In North America there are only phoxinine species, while in Europe there are mainly leuciscine species in addition to one species of bitterling, the monotypic *Tinca*, some *Gobio* species, and some *Barbus* species. In Africa there are only three subfamilies present: barbine, labeonine, and rasborine. In East Asia, especially China, all types are distributed. The specialized schizothoracine fishes are mainly found in and around the Tibetan Plateau.

Habitat

Carps can live in a large variety of habitats, from small streams and ponds to large rivers and lakes. Almost all carps live in freshwaters, although the European roach and bream (*Rutilus* and *Abramis*, respectively) have populations in the brackish part of the Baltic Sea; the Japanese *Tribolodon* spends part of its life at sea; and the Chinese carp *Cyprinus acutidorsalis* can live in the river mouth of Qingjiang River near Vietnam. *Phoxinus* and gudgeons like to stay in small streams. Big fishes like *Elopichthys bambusa* are mainly found in large rivers. *Danio* species must live in waters with temperatures higher than 64.4°F (18°C), while *Leuciscus* species only live in cold waters (39.2–71.6°F [4–22°C]). *Garra* and *Labeo* species like to adhere to the bottoms of streams and rivers with fast running water. Bitterlings prefer still or slow running waters such as ponds and lakes. *Culter* fishes often swim in the upper parts of waters or near the surface to catch insects, but the common carp and crucian carp mainly stay at the bottom sucking worms.

Behavior

Cyprinid fishes have good vision, including color vision, and use visual displays. The use of pheromones in cyprinid social communication is well established. For instance, they have an ability called fright reaction. When threatened by a predator, an individual may release alarm substances through specialized goblet or club cells in the skin. These secretions cause the other fishes nearby to disperse and hide. In this way, the rest of the group can avoid the predator. Cypriniform fishes also have excellent hearing. Shoaling minnows find food more quickly in groups and are less vulnerable to



Fancy "domestic" Japanese koi varieties: a. wild type *Cyprinus carpio*; b. Orenji ogon; c. Kohaku; d. Asagi; e. Taisho sanshoku (sanke); f. Hi utsuri; g. Ki bekko; h. Shiro bekko. (Illustration by Jacqueline Mahannah)

predation. Though some species like to search for food solitarily, in the spring they may form schools for reproduction, and in fall or winter they may transfer to deeper water as water levels decline.

Some species exhibit territorial behavior. For example, in breeding season, the male of the bitterling species, *Rhodeus ocellatus*, may find a good mussel and protect the area around this mussel as his territory.

Living only in freshwater, cyprinids need not migrate between fresh and marine waters. But some species can swim for very long distances (up to 1,012 mi [1,629 km]). Some East Asian groups undergo river and lake migration. These fishes spawn in the middle or upper reaches of rivers when heavy flood occurs. Their eggs float with the running water and hatch. The fries also float with the running water in the first few days after hatching, before running into lakes that connect to the rivers. The young fish then may stay in the lakes to take advantage of the abundance of food. When they mature, they will migrate to the rivers to breed.

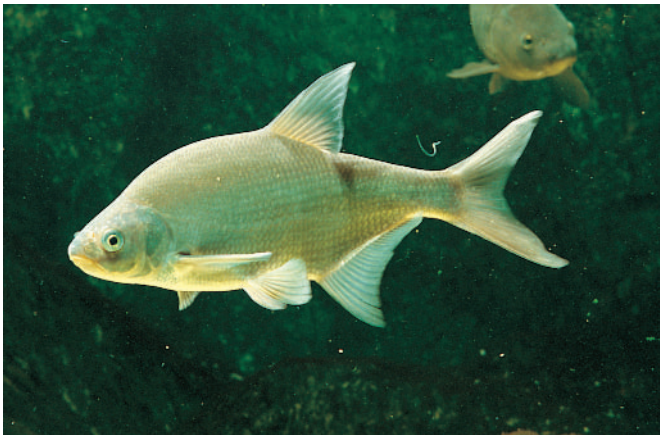
Feeding ecology and diet

Cyprinids comprise a wide variety of specialists and generalists feeding on all trophic levels. Most feed on secondary producers: zooplankton, crustaceans, larvae, pupae and adults of insects, oligochaetes, bryozoans, snails, and mussels. Some also consume primary (macrophytes and phytoplankton) or tertiary (fishes) producers. According to feeding behavior, cyprinids can be categorized into three modes: herbivores, pelagic feeders, and benthic feeders. Herbivores like grass carp eat not only aquatic plants but also the land grasses submerged by flood water. *Condrostoma* and *Xenocypris*, for example, use the horny edge on their lower jaws to scrape the algae on the bottom. Pelagic feeders mainly catch zooplankton and surface insects, but *Elopichthys bambusa* and the Colorado pikeminnow are very ferocious and feed on fishes. Some species, like silver carp and bighead carp, have evolved special gill organs for filtering plankton. *Pectenocypris balaena* of the Kapuas River in Borneo has up to at least 212 gill rakers for filtering phytoplankton. Benthic feeders suck in the sediment particles together with the organisms and separate the

A central stoneroller (*Campostoma anomalum*) male moves pebbles from the riverbed with his mouth to build a breeding nest. A group of females watches at a distance and will rush in to spawn on the nest at the same time. Another male builds his nest in the distance. (Illustration by Bruce Worden)

organisms in the pharyngeal slit. Sediment particles pass through the sieve, whereas food organisms are retained. Substratum particles too large to pass the basket are spit out.

None of the cyprinids are strictly monophagous, but many may feed on only one type of food organism, depending on availability. The feeding of European cyprinids includes all diets and feeding modes. The cyprinids from Asia seem to have the greatest variety in feeding specialists with both small and large species, whereas the cyprinids in North America have the smallest variety. Cyprinids in Africa are comprise a relatively small variety of feeding types.

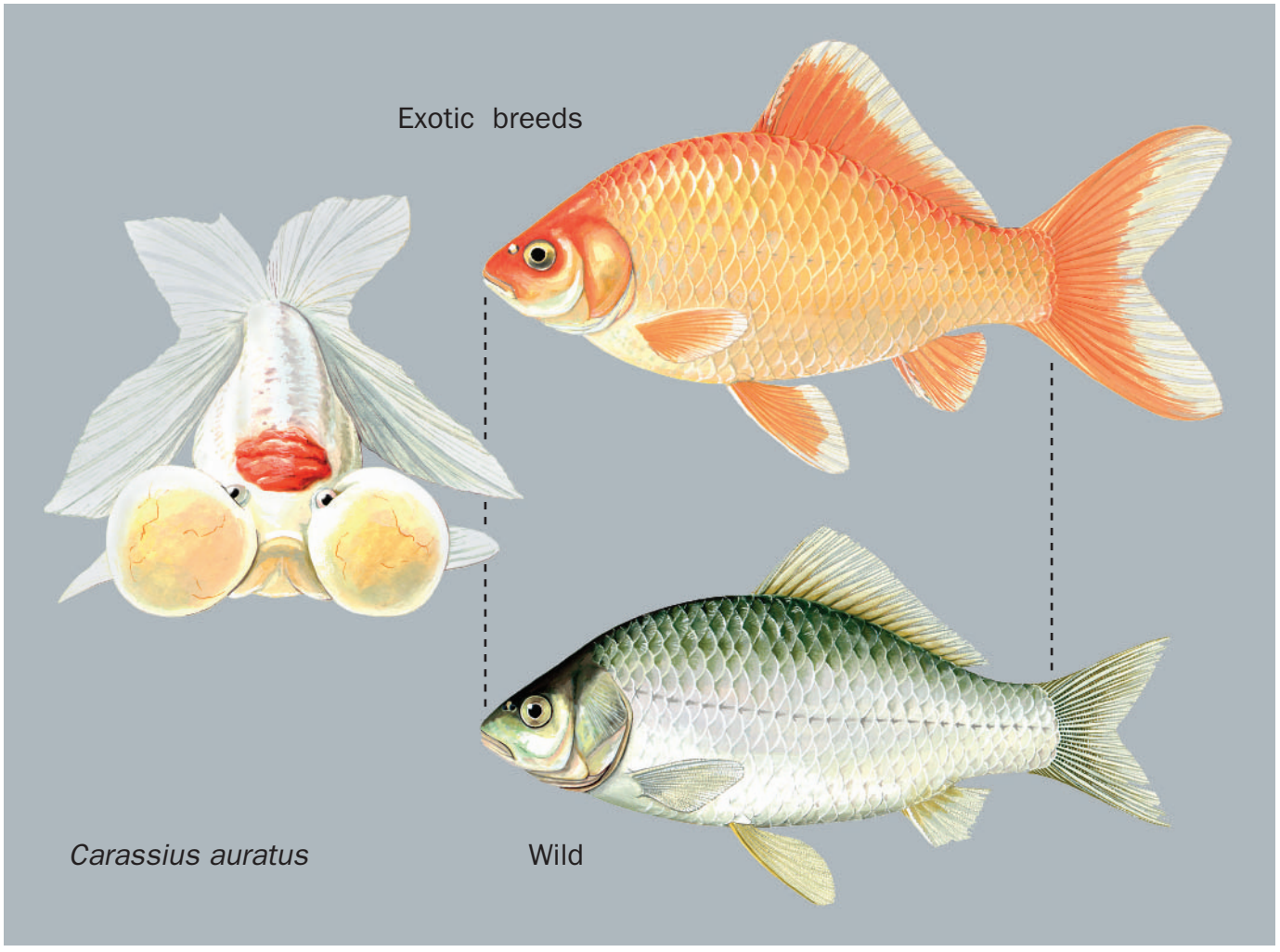


Carp bream (*Abramis brama*) live in Asia and Europe. (Photo by Y. Lanceau/Photo Researchers, Inc. Reproduced by permission.)

There is an interesting ontogenetic switch of the feeding mode in cyprinids. Almost all cyprinids start to feed on plankton shortly after hatching. As individuals increase in size, their prey choice changes, and they differentiate into the specialized feeding modes (herbivore, piscivore, and benthivore).

Reproductive biology

Carps and minnows mostly spawn in spring and summer, because the larvae will get food easily. One bitterling species breeds in autumn, which is an alternative strategy. The water temperature for reproduction may be as low as 44.6–48.2°F (7–9°C) for cold water species but must be above 64.4°F (18°C) for most East Asian groups. During breeding season, the males usually have beautiful color, for example an orange tail or anal fin to stimulate or attract females. Some species may have tubercles on the head or pectoral fin called



A colorful aquarium goldfish, *Carassius auratus*, selected for its color and fin size (top and left), compared to a much duller wild one (bottom) of the same species. (Illustration by Emily Damstra)

pearl organs, which can be used to provide tactile stimulation during courtship by pushing the female.

Usually, when their conditions are suitable, the males chase the females and press up against their abdomens. During this activity the fishes swim at very high speeds. The females then lay eggs, and the males release their sperm. Environmental conditions that impact fertilization include water temperature as well as the nature of the substances that the eggs adhere to, whether they are aquatic plants, stones, or other substances. Grass carp only spawn after heavy floods and when the water temperature is above 64.4°F (18°C); the flood surge is needed to carry eggs and larvae. Otherwise, the eggs may sink to the bottom and die.

Some cyprinids have adopted unusual breeding habits. A small minnow in southwestern China, *Gobiocypris rarus*, pushes the eggs to adhere to walls above water level through the beating of its tail. The female bitterling species lay their eggs into the gill chambers of mussels through a long tube (ovipositor).

In breeding season, the males of North American minnow known as the stoneroller dig spawning pits by driving their heads into the gravel. They transport gravel from the pits by nudging stones out with their snouts, or by transporting them with their mouths. The males compete aggressively for favored spawning areas. Male fathead minnows select nest sites under rocks or logs and they excavate the area to increase the available space, and then defend the nests aggressively from all other fatheads. After the female lays her sticky eggs on the underside of the nest object, the male fertilizes the eggs and guards the incubating eggs. He even fans them with his fins and massages them with his back pad to keep them clean and well oxygenated.

Spawning minnows of some species of *Luxilus*, *Cyprinella*, *Notemigonus*, and *Notropis* use the nests of other species of cyprinids or of species of the family Centrarchidae to deposit their eggs and leave the embryos to the protection of the host.

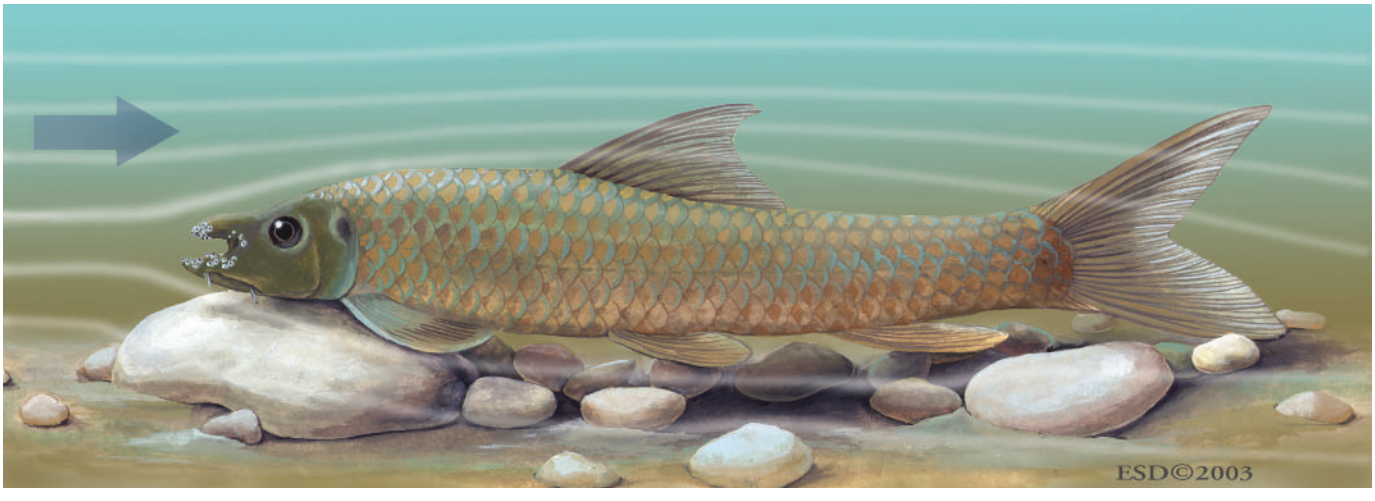
Many species spawn only one time in a single breeding season, but some species (e.g., common carps, the bitterling

The female fathead minnow (*Pimephales promelas*) lays her eggs on the underside of a lilypad. The male (shown here) cleans and aerates the eggs with the spongy tissue and tubercles it acquires on its head and neck during the breeding season. (Illustration by Emily Damstra)

fishes) have developed a strategy to spawn more than one time in a breeding season. Some species can even spawn for the whole year at an interval of 3 to 15 days.

The eggs of many species are adhesive, sticking to stones or aquatic plants. Eggs are semi-pelagic in some East Asian groups (grass carp, silver carp): the eggs sink to the bottom in still water but float with the current in running water.

The duration of development differs from species to species depending on water temperature. At 44.6°F (7°C), roach eggs take 30 days to hatch and dace eggs take 44 days. At 59°F (15°C), by contrast, only 14 days are needed for dace eggs to hatch. When temperature is 68–77°F (20–25°C), common carp eggs take 2.5–3 days to hatch. For the first few days after hatching, the larvae can not swim. Several days later, the air-bladder begins to fill with air, the yolk-sac is nearly gone,



The warty, furrowed snout of some cyprinids (including *Garra orientalis,* shown here) may provide a hydrodynamic advantage, allowing the fish to "sit" more securely in rapidly moving water. Arrow indicates direction of water flow. (Illustration by Emily Damstra)

and the larva begins to swim freely and catch food, usually plankton.

Conservation status

The IUCN Red List contains 252 species of cyprinids. Of these, 15 are categorized as Extinct; 1 as Extinct in the Wild; 39 as Critically Endangered; 31 as Endangered; 89 as Vulnerable; 6 as Lower Risk/Conservation Dependent; 23 as Lower Risk/Near Threatened; and 48 as Data Deficient. Of the 15 extinct species, 12 are from the Americas, 1 from East Asia, 1 from the Middle East, and 1 from Europe.

Major threats to cyprinids are habitat destruction, such as the construction of dams that cut off the migration routes; the eutrophication in lakes that destroys the aquatic plants necessary for cyprinid spawning; and the decrease of water area due to economic development. In addition, overfishing and competition for water resources with agricultural irrigation are also important factors threatening cyprinids. In recent years, the threat due to the introduction of exotic non-native species has become more serious.

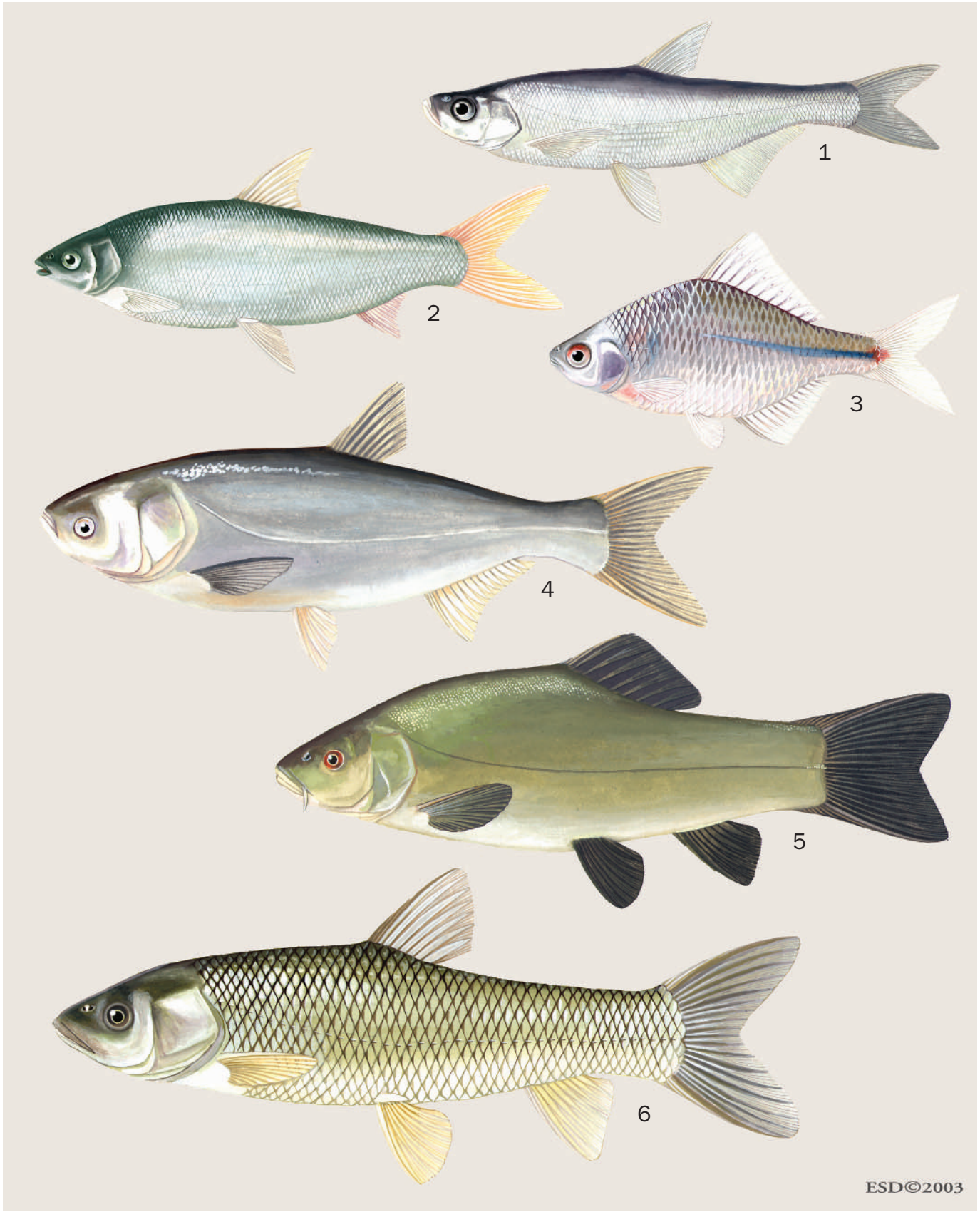
Significance to humans

Cyprinids are an important food fish. According to an FAO (Food and Agriculture Organization of the United Nations) production report for the year 1996, there were 4 cyprinid species among the top 10 species or species groups: silver carp, grass carp, common carp, and bighead carp. Cyprinids are also important in sport fishing, especially the barbel in Europe and the common carp, crucian carp, and grass carp in Asia. One cyprinid, the zebrafish, has become one of the most important model fishes in genetics and medical research.

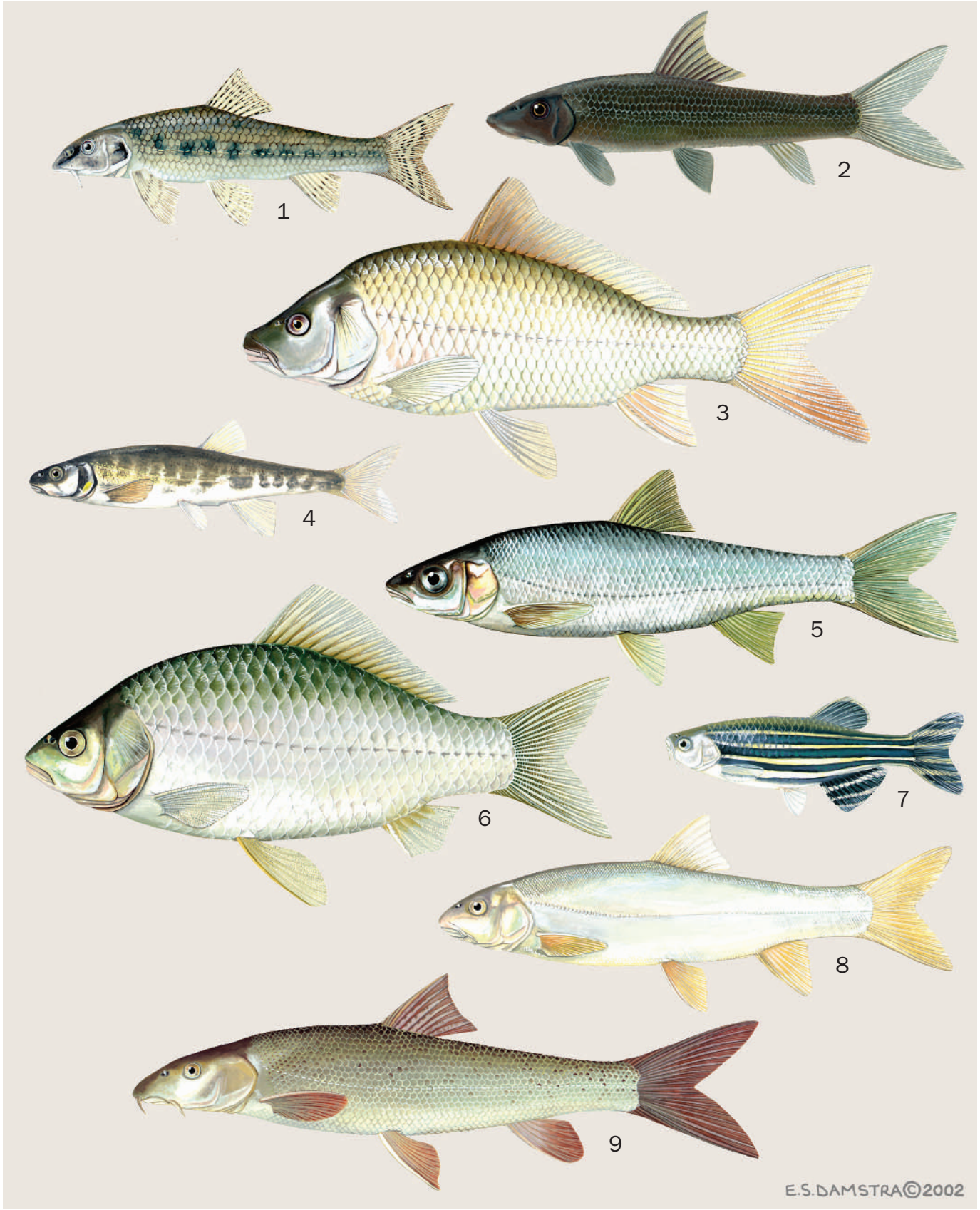
Many cyprinids are important aquarium pets. Good examples are goldfish, zebrafish, and other danios, small barbs, rasboras, and bitterlings. The Japanese colored carp, koi, is cultured in ponds as an ornamental fish. After many years of selection, the Japanese koi and Chinese goldfish have become very different from their wild types.

Grass carp have been introduced to many countries to control aquatic vegetation. Phytoplankton eaters such as the silver carp, have been used to control eutrophication in some countries. However, the introduction of carp species has also had negative effects, including the destruction of native fish fauna because of the competition for food and/or habitat changes, such as the decrease of aquatic vegetation.

1. Dagaa (*Rastrineobola argentea*); 2. Stoneroller (*Campostoma anomalum*); 3. Ningu (*Labeo victorianus*); 4. Harlequin (*Rasbora heteromorpha*); 5. Rudd (*Scardinius erythrophthalmus*); 6. Fathead minnow (*Pimephales promelas*); 7. Tiger barb (*Puntius tetrazona tetrazona*); 8. Colorado pikeminnow (*Ptychocheilus lucius*). (Illustration by Emily Damstra)



1. Upper mouth (*Culter alburnus*); 2. Smallscale yellowfin (*Xenocypris microlepis*); 3. Rosy bitterling (*Rhodeus ocellatus*); 4. Silver carp (*Hypophthalmichthys molitrix*); 5. Tench (*Tinca tinca*); 6. Grass carp (*Ctenopharyngodon idellus*). (Illustration by Emily Damstra)



1. Gudgeon (*Gobio gobio*); 2. Black stick (*Garra pingi*); 3. Common carp (*Cyprinus carpio*); 4. Eurasian minnow (*Phoxinus phoxinus*); 5. Common dace (*Leuciscus leuciscus*); 6. Crucian carp (*Carassius auratus*); 7. Zebrafish (*Danio rerio*); 8. *Schizothorax prenanti*; 9. Barbel (*Barbus barbus*). (Illustration by Emily Damstra)

Species accounts

Barbel
Barbus barbus

FAMILY
Cyprinidae

TAXONOMY
Cyprinus barbus Linnaeus, 1758, Europe.

OTHER COMMON NAMES
French: Barbet; German: Barbern.

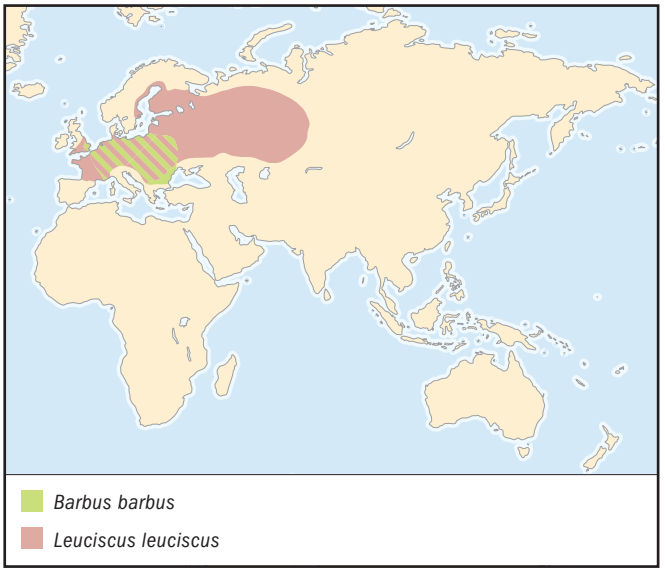
PHYSICAL CHARACTERISTICS
Size large, usually up to 29.92 in (76 cm) in length. Body long. Snout pointed. Mouth inferior. Lips fleshy. Barbels 2 pairs. Pharyngeal teeth in three rows. Dorsal fin with 4 unbranched, 7–9 branched rays; anal fin with 3 unbranched, 5 branched rays. Lateral line complete, with 56–65 scales. Vertebrae 46–47. Brown-green above, green-yellow lower sides, white-yellow belly. Covered with dark-brown spots.

DISTRIBUTION
West and Central Europe excluding Italian, Greek and Iberian peninsulas.

HABITAT
Deep, fast-flowing upper reaches of rivers with stony or gravel bottoms (barbel zones). Common temperature is 59–71.6°F (15–22°C).

BEHAVIOR
Barbels normally occur in groups of several individuals close to the river bed, but they do not congregate in schools. They migrate in rivers with a home range of 1.24–12.43 mi (2–20 km).

FEEDING ECOLOGY AND DIET
Feeds chiefly on benthic invertebrates such as small crustaceans, insect larvae, mollusks, mayfly and midge larvae, and small fishes.



REPRODUCTIVE BIOLOGY
Males mature in the fourth year and females in the fifth year of life. After the fish have migrated upriver, spawning occurs from May to July when water temperature is 57.2–68°F (14–20°C) and the bottom is filled with sand and pebbles. Eggs are firmly attached to stones. Fecundity is 8,000–12,000 eggs per kilogram of body weight.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
An important food fish and sport fish, particularly in Europe. ◆

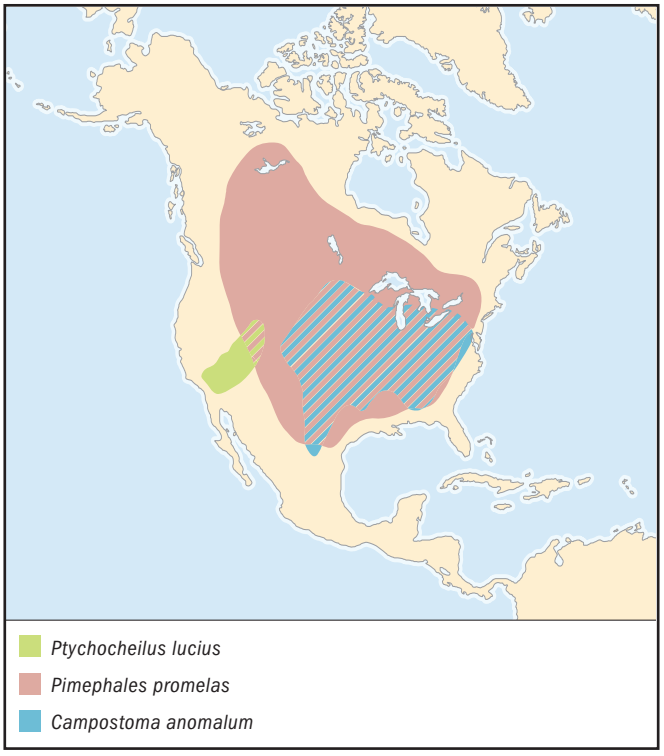
Stoneroller
Campostoma anomalum

FAMILY
Cyprinidae

TAXONOMY
Rutilus anomalous Rafinesque, 1820, Licking River, Kentucky, Ohio River drainage, United States.

OTHER COMMON NAMES
English: Central stoneroller, largescale stoneroller.

PHYSICAL CHARACTERISTICS
Size small to moderate, maximum 7.87 in (20 cm) in total length. Body stout and moderately compressed, with the nape



region becoming swollen and prominent in adults. Snout bluntly rounded and projecting beyond the nearly horizontal mouth. Lower jaw has spade-like extension. Scales deep, rather small, and crowed anteriorly; more or less mottled with dark background; scales in lateral line 53. Dorsal fin with 8 branched rays; anal fin with 7 branched rays. Color brownish, with a brassy luster above. Dusky vertical bar behind the opercle; dorsal and anal fins each with a dusky crossbar about half way up, the rest of the fin is olive in females and fiery red in males in spring. In the spring, the head and sometimes the entire body of males are covered with large rounded tubercles.

DISTRIBUTION
North America, widespread across most of eastern and central United States in Atlantic, Great Lakes, Mississippi River, and Hudson Bay basins from New York west to North Dakota and Wyoming and south to South Carolina and Texas; Thames River system in Canada; from Galveston Bay in Texas to Rio Grande in Mexico.

HABITAT
Moderate to high gradient streams with sandy to gravely substrate. Prefers riffle areas where riffles and pools alternate in rapid succession. However, can survive in almost any stream with a food supply.

BEHAVIOR
Shoaling species.

FEEDING ECOLOGY AND DIET
Primarily herbivorous, feeding diurnally on filamentous algae and diatoms but also taking detritus and aquatic insects from the periphyton assemblage on rock surfaces. Because of its long intestine (up to 8 times its body length), this species is incredibly efficient at digesting detritus and algae.

REPRODUCTIVE BIOLOGY
Matures in second or third summer of life. Adults spawn between March and late May, when water temperatures are from 55.4–80.6°F (13–27°C). Males dig spawning pits in shallow, swift riffles and occasionally in quiet pools by driving their heads into the gravel. They transport gravel from the pits by nudging stones out with their snouts (hence the name *stoneroller*) or by transporting them with their mouths. Males compete aggressively for favored spawning areas. Females remain in deeper water near the spawning pits and enter the pits individually or in groups to deposit eggs. The adhesive eggs become lodged in the gravel and are abandoned prior to hatching.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Not sought by anglers. They do make good bait but are difficult to culture. ◆

Crucian carp
Carassius auratus

FAMILY
Cyprinidae

TAXONOMY
Cyprinus auratus Linnaeus, 1758, China, Japanese rivers.

OTHER COMMON NAMES
English: Goldfish, golden carp.

PHYSICAL CHARACTERISTICS
Size small to moderate, normally 5.12–7.48 in (13–19 cm) in standard length. Body deep and stout, moderately compressed. Snout pointed. Mouth terminate, oblique. Barbels absent. Pharyngeal teeth in one row. Gill rakers 37–43. Dorsal fin long, 4 spines, 15–19 rays. Anal fin short, 3 spines, 5 rays. Back of last dorsal and anal spines serrated. Lateral line complete, with 27–30 scales. Wild forms are usually olive-green in the back, gray-white on belly.

There are many aquarium varieties in different forms and colors. These can be divided into four types: (1) Grass type: primitive with slender body, pointed head, small eyes, and single or double tails; (2) Fancy type, with double tails and all fins very long; (3) Dragon or Eye type, with large eyes that protrude out; (4) Egg-shaped type, with the dorsal fin absent.

DISTRIBUTION
Native to Asia. The wild type has been introduced to Europe and North America. Aquarium varieties have been introduced all over the world.

HABITAT
Shallow, warm waters with dense vegetation such as lakes, reservoirs, and streams. Adults are generally found near the bottom, but they sometimes appear in schools at the surface.

BEHAVIOR
The social behavior of crucian carp is similar to that of the common carp, but under some conditions it can attain a greater population density.

FEEDING ECOLOGY AND DIET
Omnivorous, consuming a variety of larvae and aquatic insects, mollusks, crustaceans, aquatic worms, and aquatic vegetation.

REPRODUCTIVE BIOLOGY
The crucian carp matures after the body length reaches 3.54 in (9 cm) in the first or second year. Spawning occurs in spring when the water temperature reaches 60.08°F (15.6°C) and heavy rains occur. The eggs are released in batches, and are

usually attached to aquatic plants and other fixed objects. The male fertilizes the eggs immediately. The incubation may take 4 days at 62.6–66.2°F (17–19°C). After hatching, the larvae cling to plants or remain quietly on the bottom, but after 1–2 days they become free-swimming. Fecundity varies from 12,000 to 28,000 eggs per individual.

CONSERVATION STATUS
Not listed by the IUCN. Due to artificial hybridization and transplantation, local types have been seriously damaged.

SIGNIFICANCE TO HUMANS
An important food fish, although its production is much less than that of the common carp. Its greatest value is as an aquarium fish. ◆

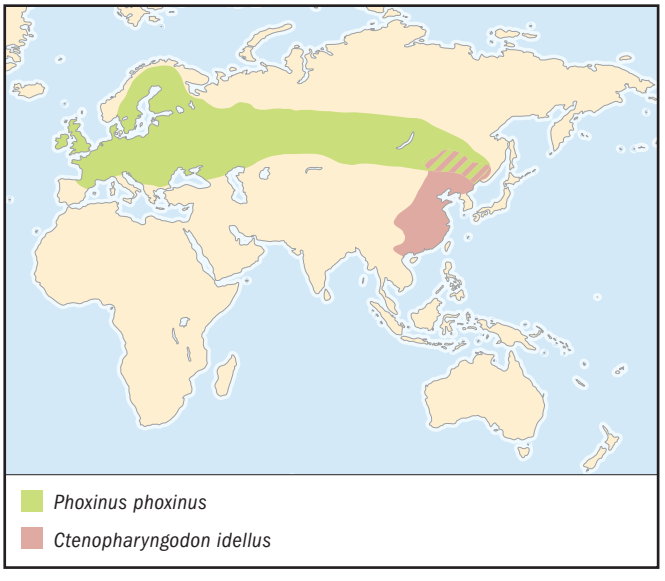
Grass carp
Ctenopharyngodon idellus

FAMILY
Cyprinidae

TAXONOMY
Leuciscus idella Cuvier and Valenciennes, 1844, China.

OTHER COMMON NAMES
English: White amur; French: Amour blanc; German: Graskarpfen; Spanish: Carpa herbivora.

PHYSICAL CHARACTERISTICS
Size large, commonly 9.84–35.43 in (25–90 cm) in body length. Body long, cylindrical in the front, compressed in the hind. Belly round. Snout short and blunt. Mouth terminal, large and wide. Barbels absent. Pharyngeal teeth in 2 rows, larger ones compressed like a comb. Gill rakers 14–18. Dorsal fin short, with 3 unbranched, 7 branched rays. Anal fin with 3 unbranched, 8–9 branched rays. Scales moderate, lateral line complete, with 35–42 scales. Coloration brassy olive above, white on lower sides and belly. Edge of scales dark gray. Pectoral and ventral fins gray-yellow, other fins gray.



DISTRIBUTION
East Asia, from Amur River to Yellow River, Yangtze River, and Pearl River. Widely transported around the world.

HABITAT
Lakes, ponds, pools, and backwaters of large rivers. Prefers large, slow-moving or standing water bodies with vegetation.

BEHAVIOR
Usually stay in lower depths and are solitary in nature. They mature in lakes and migrate to rivers for reproduction.

FEEDING ECOLOGY AND DIET
Mainly feeds on aquatic plants and submerged land grasses; also takes detritus, insects, and other invertebrates.

REPRODUCTIVE BIOLOGY
Grass carps usually mature in the fourth year of life. Spawning occurs in late April and early May, when water temperatures reach 64.4°F (18°C), and with the onset of heavy floods. Mature fishes swim upstream. When the water level rises suddenly, males may chase females and push them. The females then lay eggs, and males release sperm. The eggs are semi-pelagic, floating with the currents. Incubation may take 35–40 hours when temperature is 66.92–70.16°F (19.4–21.2°C). Fecundity is 306,578–1,162,920 eggs, depending on the size of the adult female.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
One of the world's most important aquaculture species. Also used for weed control in rivers, fish ponds, and reservoirs. ◆

Upper mouth
Culter alburnus

FAMILY
Cyprinidae

TAXONOMY
Culter alburnus Basilewsky, 1855, northern China.

OTHER COMMON NAMES
English: Whitefish, lookup.

PHYSICAL CHARACTERISTICS
Size moderate to large, 5.9–25.6 in (15–65 cm) in body length. Body long, compressed. Dorsal straight, abdomen curved. Belly is keeled from ventral base to anus. Snout blunt. Mouth extremely superior, almost vertical. Barbels absent. Pharyngeal teeth sharp, in three rows. Gill rakers long, 24–28. Dorsal fin short, with 3 unbranched, 7 branched rays; last unbranched ray is spine-like. Anal fin long, with 3 unbranched, 21–24 branched rays. Scales small. Lateral line complete, with 80–92 scales. Air bladder has 3 chambers. Back dark gray, lower sides and belly silver-white. Fins gray.

DISTRIBUTION
East Asia from Amur River to the Pearl River, and into northern Vietnam.

HABITAT
Rivers and floodplain lakes with aquatic macrophytes and slow-running water.

BEHAVIOR
Often lives in middle and upper parts of water bodies in small groups. Swims fast and likes to leap.

FEEDING ECOLOGY AND DIET
Carnivorous. Feeds on zooplankton, insects, and small fishes.

REPRODUCTIVE BIOLOGY
Males mature in the second, females in third year of life in the Yangtze River. Spawning occurs in mid-June in rivers or in shallow areas of lakes. Eggs are slightly attached to aquatic plants and may be detached and sink to the bottom due to wave movements. Fecundity varies from 51,490 to 532,350 eggs.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
An important food fish in the floodplain area of China. ◆

Common carp
Cyprinus carpio

FAMILY
Cyprinidae

TAXONOMY
Cyprinus carpio Linnaeus, 1758, Europe.

OTHER COMMON NAMES
English: Carp, German carp, European carp, mirror carp, leather carp, leatherback, German bass.

PHYSICAL CHARACTERISTICS
Size moderate to large, usually 11.8–15.74 in (30–40 cm) in body length. Body robust, compressed laterally. Snout long; mouth of moderate size reaching to below nostril. Two barbels on each side of upper jaw, smaller one from edge of snout, larger one near corner of mouth. Pharyngeal teeth in three rows; larger teeth molarlike. Gill rakers 21–27. Dorsal fin long, 4 spines, 15–23 branched rays; anal fin short, 3 spines, 5 branched rays. Back of last dorsal and anal spines serrated. Lateral line complete, with 32–41 scales. The usual longevity of the carp is 9–15 years; maximum observed longevity is 47 years. Brassy olive above, lower sides golden yellow; belly yellow-white. Basal half of caudal and anal fins often reddish; stronger coloration in adults.

DISTRIBUTION
Native to Asia from the Amur River to North Vietnam. It was carried to Europe just before and after the beginning of the common era. Its introduction to the American continent took place during the first half of the nineteenth century. By now it has been transplanted all over the world.

HABITAT
Lives in a wide variety of habitats, including ponds, lakes, streams, and large rivers. It can tolerate a very low concentration of oxygen and high salinity. Normally, it prefers shallow, warm waters with aquatic plants over cold, small streams with fast-running water.

BEHAVIOR
Usually live in lower part or bottom of waters. In spring and autumn, they form schools. Though they need not migrate to rivers for reproduction, some fish can swim very long distances (up to 1,012 mi [1,629 km]).

FEEDING ECOLOGY AND DIET
Typically omnivorous and a benthic feeder. Food diet includes macrophytes, detritus and algae, molluscs, aquatic insects and their larvae, minute crustaceans, and small fishes.

REPRODUCTIVE BIOLOGY
Males mature usually by the second year of life in Asia, third or fourth year in Europe. Females require an additional year for maturation. Spawning may occur when water temperature reaches 64.4°F (18°C). Another prerequisite for spawning is

the vegetation. Flood waters usually stimulate spawning. Spawning groups are composed of one female and one or more males. The males initiate the spawning act by repeatedly pushing their heads against the body of the female. On stimulation by the males, the female responds by raising her caudal peduncle and tail. Her tail lashes violently, and as she propels herself forward, she scatters the eggs over the vegetation. Simultaneously, the males come along the side of the female with their tail region proximate to the female genital opening and, by violent movements of their tail region, discharge their milts. The eggs are released gradually, in batches of 3–4, within a period of 3–4 days if the weather is good, or 2 to 3 weeks if spawning is interrupted by cold, cloudy, or windy spells. The eggs are attached to the vegetation and hatch after 2.5 to 3 days (water temperature 68–77°F [20–25°C]). For the first two days after hatching, the larvae stay on the grass quietly. On the third day, their air-bladders begin to get air. On the fourth day, the yolk-sac is nearly gone and the larvae begin to feed. The period of planktonic feeding is short; juveniles take invertebrate food from the bottom after reaching a length of 0.79 in (2 cm). Forty days later, with the body covered with scales and barbels appearing, the fish look very much like adults. Fecundity varies from 59,000 to 1,579,000 eggs per individual.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN. Due to artificial hybridization and transplantation, the genetic resources of common carp have been seriously damaged. Many different local varieties (e.g., red carp, glass carp) have been contaminated genetically.

SIGNIFICANCE TO HUMANS
This is the earliest domesticated fish species. Ancient Chinese began to culture the common carp around 200 B.C. As this species is considered a symbol of happiness and good fortune in China, it is still common as wedding gift, particularly in rural areas. The Japanese colored carp, koi, had its origin in Japan between A.D. 794 and 1184. It is now one of the most common ornamental fishes in the world.

Some local varieties are important as a source of food, while others are important in the aquarium trade. The common carp is also an important game fish.

Zebrafish
Danio rerio

FAMILY
Cyprinidae

TAXONOMY
Cyprinus rerio Hamilton, 1822, Kosi River, Utter Pradesh, India.

OTHER COMMON NAMES
English: Zebra danio, striped danio; German: Zebrabärbling.

PHYSICAL CHARACTERISTICS
Small fish, rarely grows beyond 1.97–2.36 in (50–60 mm) in length. Body slender, slightly compressed. Two pairs of barbels: rostral barbels extend to anterior margin of orbit; maxillary barbels end at about middle of opercle. Dorsal fin with 3 unbranched, 7 branched rays. Anal fin striped, with 3 unbranched, 10–12 branched rays. Lateral line incomplete or absent. Vertebrae 31–32. Body silvery, sometimes tinted with gold, with five blue horizontal stripes on the sides. Stripes also present in the anal and caudal fins.

DISTRIBUTION
Native to tributaries of the Ganges River, along the Coromandel Coast of India, from Calcutta to Masulipatam, Bengal, Nepal, Pakistan, and Bangladesh. As aquarium fish and experimental animal, it has been introduced worldwide.

HABITAT
Slow-moving and still water bodies such as streams, canals, ditches, and ponds, particularly rice fields.

BEHAVIOR
Very active, usually swimming in schools.

FEEDING ECOLOGY AND DIET
Feeds mainly on worms and small crustaceans. It also feeds on insect larvae and can be used for mosquito control.

REPRODUCTIVE BIOLOGY
Matures in 4–6 months. Females are larger and have less vibrant coloration than males. Typically, spawning occurs in the early hours of the morning. Eggs are semiadhesive, relatively large, and released into open waters. Under experimental conditions, this species spawns at intervals of 1.9 to 2.7 days. However, spawning intervals in nature are typically much longer, varying from 5 days to several weeks. Between 21 and 60 eggs are released per spawning event. In captivity, the total number of eggs spawned is usually between 400 and 500. Eggs hatch approximately 20–48 hours after spawning. Larvae live from 48 to 72 hours on their yolk-sac provision.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Because of their small size, zebrafish are of no value as a food fish. However, they are very popular aquarium fish and also very important as experimental subjects for genomic study. ◆

Black stick
Garra pingi

FAMILY
Cyprinidae

TAXONOMY
Garra pingi Tchang, 1929, Katin, Szechuan, China.

OTHER COMMON NAMES
German: Pings Saugbarbe.

PHYSICAL CHARACTERISTICS
Size small to moderate, normally 2.76–10.6 in (7–27 cm) in body length. Body slender, slightly cylindrical in the front, and compressed in the hind. Snout round, blunt. Mouth inferior, transverse. Lower lip specialized as disc. Barbels absent in adults. Pharyngeal teeth very small, in three rows. Gill rakers 36–44. Dorsal fin short, 2 unbranched, 9 branched rays; anal fin has 2 unbranched and 5 branched rays. Lateral line complete, with 48–52 scales. Dark black above, gray black on the lower sides; gray-white on belly. Bases of scales have black spots.

DISTRIBUTION
Upper reaches of the Yangtze, Pearl, and Mekong Rivers in Southeast Asia.

HABITAT
Lives in upper reaches of rivers with fast-running water and stony bottoms. Limited to warm waters.

BEHAVIOR
Normally adheres to the stony bottom with the sucking disc formed by lower lip. Very active.

FEEDING ECOLOGY AND DIET
Mainly scrapes algae and fragmental plants, but also feeds on insect larvae.

REPRODUCTIVE BIOLOGY
Little is known.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Used for food, but the production is very low. ◆

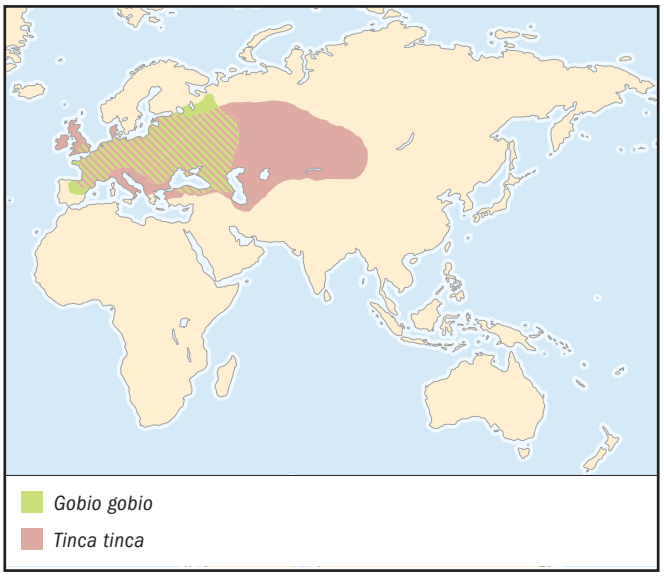
Gudgeon
Gobio gobio

FAMILY
Cyprinidae

TAXONOMY
Cyprinus gobio Linnaeus, 1758, Britain and surrounding countries.

OTHER COMMON NAMES
French: Gofi, goujon; German: Grässling; Spanish: Gobio.

PHYSICAL CHARACTERISTICS
Small fish, length rarely exceeding 5.9 in (15 cm); maximum age 8 years. Body slender, round in front, compressed laterally toward the tail. Snout blunt. Mouth inferior. Barbels one pair. Pharyngeal teeth in 2 rows. Dorsal fin with 3 unbranched, 5–7 branched rays; anal fin with 3 unbranched, 6 branched rays. Lateral line complete, with 40–45 scales. Vertebrae 39–41. Brown-grey above, sides lighter, yellowish-white belly. On the sides there is a row of large, indistinct dark marks. Dorsal and tail fins are spotted.



DISTRIBUTION
Europe.

HABITAT
Fast-flowing rivers with sand or gravel bottoms; may also occur in still waters.

BEHAVIOR
Often appear in large numbers. Normally active during the day, but if they are disturbed, in particular by predators, they can defer their activity to periods when light intensity is weak. They are capable of emitting squeaking sounds.

FEEDING ECOLOGY AND DIET
Bottom feeder. Usually active during summer months. Its diet includes insect larvae, mollusks, and freshwater shrimps.

REPRODUCTIVE BIOLOGY
Matures in 2–3 years. The spawning time is from April to August, when temperatures are above 62.6°F (17°C). The fecundity is 2,500–6,500 eggs per individual.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
The gudgeon's chief value is as bait for larger fish. Its flesh is tasty, but its small size reduces its value as food. ◆

Silver carp
Hypophthalmichthys molitrix

FAMILY
Cyprinidae

TAXONOMY
Leuciscus molitrix Cuvier and Valencinnes, 1844, China.

OTHER COMMON NAMES
English: Chinese schemer; French: Carpe argentée; German: Silberkarpfen, Tolstolob; Spanish: Carpa plateada.

PHYSICAL CHARACTERISTICS
Size moderate to large, usually 11.8–15.74 in (30–40 cm) in body length. Body robust, compressed laterally. Keels from isthmus to anus on the belly. Head large. Snout blunt. Mouth terminal, wide and large. Barbels absent. Pharyngeal teeth in 1 row. Contains spiral gill-organ for feeding. Dorsal fin short, with 3 unbranched, 7 branched rays; anal fin long, with 3 unbranched 11–13 branched rays. Scales small. Lateral line complete, with 91–120 scales. Coloration is brassy olive above, and silver-white on lower sides and belly.

DISTRIBUTION
China and eastern Siberia. Introduced around the world for aquaculture and control of algal blooms.

HABITAT
Can live in standing or flowing waters such as ponds, lakes, and rivers. Prefers large waters with abundant plankton.

BEHAVIOR
Active species well known for its habit of leaping clear of the water when disturbed. It often swims just beneath the water surface. Undergoes lake-river migration.

FEEDING ECOLOGY AND DIET
Typical filter feeder that lives near the surface and feeds on phytoplankton and microzooplankton with its big mouth and the gill organ.

REPRODUCTIVE BIOLOGY
In Yangtze River, this fish matures in 3–4 years. Breeding season is from April to July. The fish migrate to middle or upper reaches of the river to breed. Spawning occurs near the surface of water. The eggs are semipelagic. Eggs and larvae float downstream to floodplain zones. The fecundity varies from 207,083 to 1,610,440 eggs.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
The silver carp is an important food fish and has been introduced to many countries. It is among the 4 species of cyprinids whose world production in aquaculture exceeds 1 million tons per year. However, in some places it is mainly used for cleaning reservoirs and other waters where eutrophication is a problem. ◆

Ningu
Labeo victorianus

FAMILY
Cyprinidae

TAXONOMY
Labeo victorianus Boulenger, 1901, Lake Victoria Nyanza, East Africa.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Size small to moderate, maximum 15.75 in (40 cm) in standard length. Body long, slightly compressed. Snout profile smooth and rounded. Jaws with horny cutting ridge, with flap of skin in front of upper lip. Barbels hidden. Dorsal fin with 9–10 branched fin rays. Lateral line running along middle of the flank and the caudal peduncle; scales in lateral line 36–39. Olive dorsally, cream-colored ventrally. Dorsal, anal, and pelvic fins often orange-tipped.

DISTRIBUTION
East Africa: Lake Victoria (Nile drainage basin).

HABITAT
Shallow inshore waters and influent rivers.

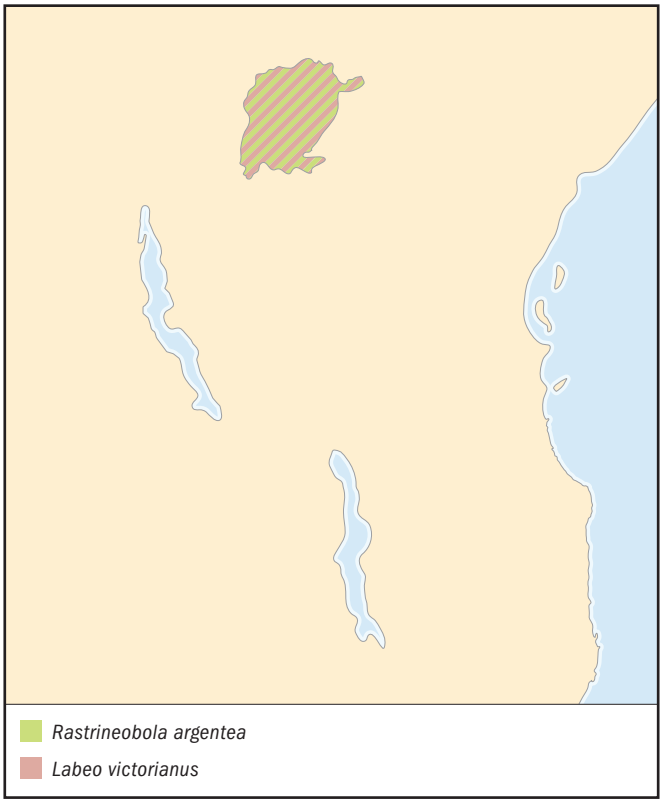
BEHAVIOR
Spends most of its life span in lakes, but migrates to spawn in flooded grasslands beside both permanent and temporary streams.

FEEDING ECOLOGY AND DIET
Feeds on detritus and algae. Also feeds on rotifers growing on the bodies of other fishes.

REPRODUCTIVE BIOLOGY
Migrates to rivers to spawn in flood season.

CONSERVATION STATUS
Not listed by IUCN. This species has been adversely affected by overfishing and predation by the introduced Nile perch.

SIGNIFICANCE TO HUMANS
Important food fish. ◆



Common dace
Leuciscus leuciscus

FAMILY
Cyprinidae

TAXONOMY
Cyprinus leuciscus Linnaeus, 1758, Central Europe.

OTHER COMMON NAMES
English: Dace; French: Acourcie, assée, aubour, gandoise; German: Hasel.

PHYSICAL CHARACTERISTICS
Size small to moderate, length rarely exceeding 10.2 in (26 cm), maximum length 15.75 in (40 cm); maximum reported age is 16. Body long. Snout pointed. Mouth narrow, slightly inferior. Barbels absent. Pharyngeal teeth in 2 rows. Dorsal fin has 3 unbranched, 7–9 branched rays; anal fin has 3 unbranched, 8–9 branched rays. Lateral line complete, with 47–52 scales. Vertebrae 42–46. Dorsal part dark, sides silver, belly white.

DISTRIBUTION
Native to Europe and northern Asia. It has become widespread in Europe and gained access to Ireland as a bait fish.

HABITAT
Prefers upper reaches of rivers and especially clear, cool lakes with fast-flowing water and sand or gravel substrate.

BEHAVIOR
Usually swims near the surface in large numbers, with large home range and localized feeding migrations.

FEEDING ECOLOGY AND DIET
Feeds on insects, worms, snails, and only rarely plants. It may feed all year, intensely so at dawn and dusk.

REPRODUCTIVE BIOLOGY
Matures in 3–4 years. Reproduction occurs in March and April, when water temperature is 48.2–50°F (9–10°C), with single spawning. Eggs are pale yellow and attach to gravel and stones in shallow, flowing water. Fecundity for females is 6,500–9,500 eggs.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Not good as food fish because they are too small and bony, but they make good bait for larger fish. ◆

Eurasian minnow
Phoxinus phoxinus

FAMILY
Cyprinidae

TAXONOMY
Cyprinus phoxinus 1758 Europe.

OTHER COMMON NAMES
English: Common minnow; French: Amarante, arlequin, vairon; German: Blutelritze.

PHYSICAL CHARACTERISTICS
Small fish, length rarely exceeding 3.94 in (10 cm); maximum age 6 years. Body slender, slightly compressed. Snout short and blunt. Mouth small, terminal. Barbels absent. Pharyngeal teeth in 2 rows. Gill rakers 7–8. Dorsal fin short, with 3 unbranched, 7 branched rays; anal fin with 3 unbranched, 7 branched rays. Scales small. Lateral line incomplete, with 32–41 scales, ending before anal origin. Coloration is brassy olive above, golden yellow on lower sides, and yellow-white on belly. Basal half of caudal and anal fins often reddish; stronger coloration in adults.

DISTRIBUTION
Eurasia, from British Isles and eastern Spain to eastern Siberia and Amur River.

HABITAT
Cold yet well-oxygenated waters (running or still) over gravel substrate, mainly in rivers and streams, occasionally in lakes and canals.

BEHAVIOR
Often found in large numbers, never solitary. They may migrate upstream for spawning in shallow gravel areas.

FEEDING ECOLOGY AND DIET
Feeds on algae, plant debris, mollusks, crustaceans, zooplankton, and insect larvae. It may forage all day, and feeding takes place throughout the year.

REPRODUCTIVE BIOLOGY
Matures in 2–3 years. The spawning times are mainly from June to July, with multiple spawning. Spawning takes place over gravel and weeds. Eggs are fixed on plants or stones. Fecundity is 200–1,000 eggs per female.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
No commercial value but an important laboratory fish. ◆

Fathead minnow
Pimephales promelas

FAMILY
Cyprinidae

TAXONOMY
Pimephales promelas Rafinesque, 1820, Lexington, Kentucky, United States.

OTHER COMMON NAMES
English: Black-head minnow, rosy-red.

PHYSICAL CHARACTERISTICS
Small fish, maximum 3.94 in (10 cm) in total length. Body moderately compressed. Snout short and blunt. Mouth subterminal. Scales deep, closely overlapping. Lateral line incomplete or nearly complete, with 43–44 scales. Both dorsal and anal fin with 7 branched rays. Olive to brown on the upper body and silvery white on the lower body with a dark midlateral stripe. Nuptial males tend to be larger than females with horny tubercles on the snout and a prominent pad of spongy wrinkled tissue on the nape. One variety with light orange color named *rosy red.*

DISTRIBUTION
Native to central North America, northeastern United States, and northeastern Mexico. It has been introduced widely throughout much of North America as a bait minnow.

HABITAT
Found in a wide variety of habitats in rivers, streams, lakes, and ponds, particularly in waters with abundant floating and submerged vegetation. It has a high tolerance for turbid waters, low oxygen, and high temperatures.

BEHAVIOR
Shoaling species. Males are territorial in breeding season.

FEEDING ECOLOGY AND DIET
Feeds in soft bottom mud, taking a variety of items from algae and plant fragments to insect larvae and microscopic crustaceans.

REPRODUCTIVE BIOLOGY
Matures by about six months of age. Spawning occurs from late May to early June when water temperatures exceed 60.8°F (16°C). In breeding season, a male develops dark coloration and breeding tubercles on his head, and a soft mucus-like pad on his nape. The male selects the nest site under an object such as a log, rock, or stick, and excavates the area around the object. He then defends it aggressively from all other fatheads except egg-laden females. The female enters the nest, turns upside down, lays her sticky eggs on the underside of the nest object, and leaves the nest. The male then fertilizes the eggs and guards the incubating eggs. He fans them with his fins and massages them with his back pad to keep them clean and well oxygenated. Other females may add eggs to the nest as the spawning season progresses. The male continues his care until all of the eggs hatch. Females produce clutches of eggs. Each clutch may contain 80–370 eggs. Most females probably spawn several clutches in a season. The embryos hatch in about 4–6 days.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Often sold as bait and in aquarium stores to be used as "feeder fish." Several countries report adverse ecological impact after introduction, such as causing the spread of enteric redmouth disease, which has infected wild and cultured trouts and eels. The fathead minnow was used in the past as a form of mosquito control in some places and is still widely used as a bioassay subject. ◆

Colorado pikeminnow
Ptychocheilus lucius

FAMILY
Cyprinidae

TAXONOMY
Ptychocheilus lucius Girard, 1856, Colorado River, California, United States.

OTHER COMMON NAMES
English: Colorado squawfish.

PHYSICAL CHARACTERISTICS
Largest cyprinid in North America, maximum 71 in (180 cm) in total length. Body slender, elongate, with long, depressed head. Maxillary reaching past anterior margin of the eye. Fins moderate, both dorsal and anal fins with 9 branched rays. Scales very small; lateral line very strongly decurved; lateral line scales 83–87. Color plain, dark above. Young always have a black caudal spot and a faint pale lateral band below a darker one.

DISTRIBUTION
North America, in the Colorado River drainage in Wyoming, Colorado, Utah, New Mexico, Arizona, Nevada, and California, from the United States to Mexico. Now mostly restricted to Utah and Colorado and extirpated from the southern portion of the range by the construction of large dams on the Colorado and Gila Rivers.

HABITAT
Juveniles utilize backwater and side channel areas with little or no current and silt or sand substrates. Adults inhabit medium to large rivers, with larger ones found in deep pools with a strong current flowing over rocky or sandy substrates.

BEHAVIOR
Adults are largely solitary, except during spawning or during low flows that crowd them into reduced habitat.

FEEDING ECOLOGY AND DIET
Younger individuals feed primarily on insects and crustaceans, whereas older fish are piscivores, consuming only other fish.

REPRODUCTIVE BIOLOGY
Spawns from early July through mid-August, after water temperatures have exceeded 64.4°F (18°C) for about a month. Preferred spawning sites are apparently gravel and cobble-bottomed riffles, where the interstitial spaces are free of organic matter and sediment. Newly hatched larvae drift downstream to quiet backwaters, where they grow rapidly and then return to the main-channel habitats when they are about 3 in (7.6 cm) long.

CONSERVATION STATUS
Classified as Vulnerable by the IUCN. The near extinction of this species is due to a combination of factors, the most significant being those associated with water development projects that have altered stream morphology, flow patterns, temperatures, water chemistry, and silt loads of most major streams throughout the Colorado River basin. Also, several exotic species may prey upon and compete with Colorado pikeminnows, particularly juveniles. Finally, there have been several fish eradication projects that may have had a severe impact on local populations. A captive propagation is underway; reintroductions into the Salt and Verde drainages began in 1985.

SIGNIFICANCE TO HUMANS
This species used to be an important food fish, but now its population is too small to sustain such activities. ◆

Tiger barb
Puntius tetrazona

FAMILY
Cyprinidae

TAXONOMY
Capoeta tetrazona Bleeker, 1855, Lahat, Palembang Province, Sumatra, Indonesia.

OTHER COMMON NAMES
English: Green tiger barb, Sumatra barb, partbelt barb; German: Moosbarbe; Malay: Ikan baja.

PHYSICAL CHARACTERISTICS
Small fish, maximum 2.76 in (7 cm) in total length. Body stocky, deep, and compressed. Mouth obtuse. Barbels absent. Dorsal fin with 8–9 branched rays, anal fin with 5 branched rays. Brilliantly colored. Dorsal brown to olive in color, flanks with a delicate reddish brown luster. Scales splendidly edged with shining gold. Body covered with four black vertical bars, with the first one passing through the eye, the second just anterior to the insertion of the dorsal fin, the third posterior to the dorsal, and the fourth passing through the caudal peduncle. Dorsal and anal fins blood-red; remaining fins more or less reddish. Ventral fins are occasionally black. Besides the traditional form, albino, black, and green morphs are also seen in the aquarium industry.

DISTRIBUTION
Southeast Asia: Sumatra and Borneo. Introduced widely and has been reared in several countries in facilities for breeding aquarium fishes.

HABITAT
Shallow, warm rivers and streams.

BEHAVIOR
Lively shoaling fish. Aquarium specimens are notorious for their habit of picking at the fins of other fish.

FEEDING ECOLOGY AND DIET
Feeds on worms, small crustaceans, and plant matter.

REPRODUCTIVE BIOLOGY
Matures between 9–12 months of age. Males are smaller and more brightly colored than females. Generally from 300 to 1,000 eggs are spawned. The eggs are large and yellowish, and the fry hatch within 36 hours.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Very popular as an aquarium fish. ◆

Harlequin
Rasbora heteromorpha

FAMILY
Cyprinidae

TAXONOMY
Rasbora heteromorpha Duncker, 1904, Kuala Lumpur, Selangor, Malaysia.

OTHER COMMON NAMES
English: Red rasbora; German: Keilfleckrasbora; Finnish: Kiilakylki; Russian: Rasbora krasnaya.

PHYSICAL CHARACTERISTICS
Small fish, maximum 1.97 in (5 cm) in total length. Lateral line incomplete. Anterior part silver in color. Starting beneath the dorsal fin running to the tail, individuals are marked with a blackish blue triangular-shaped patch. This patch is slightly rounded at the bottom and ends in an extended tip in males but is straight in females. Eyes have a bright red glow. Dorsal fin vivid red with a yellow tip; tip of caudal fin bright red; inner rays yellow.

DISTRIBUTION
Thailand to Sumatra, Indonesia.

HABITAT
Small waters in rainforests.

BEHAVIOR
Shoaling species.

FEEDING ECOLOGY AND DIET
Feeds on worms, crustaceans, and insects.

REPRODUCTIVE BIOLOGY
The usual site for spawning is the underside of a broad-leafed aquatic plant. Females deposit their eggs rather than merely scattering them in the water.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Very popular as an aquarium fish. ◆

Dagaa
Rastrineobola argentea

FAMILY
Cyprinidae

TAXONOMY
Neobola argentea Pellegrin, 1904, Lake Victoria, Africa.

OTHER COMMON NAMES
English: Silver cyprinid, mukene, sardine; German: Viktoria-Sardine; Swahili: Omena.

PHYSICAL CHARACTERISTICS
Small fish, rarely reaching a length greater than 3.15 in (8 cm) in standard length. Body slender, compressed. Barbels absent. Cheeks covered by thin suborbital bones. Lateral line low on the body and running along lower part of caudal peduncle; scales in lateral line 42–56. Body silver-white with an overall nacreous sheen. Caudal fin yellow. White-blue stripe along the middle of the body side.

DISTRIBUTION
East Africa: Lakes Victoria and Kyoga and Nile River drainage basin.

HABITAT
Found inshore and offshore. Adults stay near the bottom during the day and near the surface at night.

BEHAVIOR
Shoaling species.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton and surface insects.

REPRODUCTIVE BIOLOGY
Matures in the second year of life and spawns near the shore. Juvenile fish migrate away from the shore after spending their larval stage in shallow areas.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
One of the three most important commercial species in Lake Victoria. It is a cheap source of protein food for direct human consumption and also an important food item for larger fishes in the lake. ◆

Rosy bitterling
Rhodeus ocellatus

FAMILY
Cyprinidae

TAXONOMY
Pseudoperilampus ocellatus Kner, 1866, Shanghai, China.

OTHER COMMON NAMES
German: Hongkong Bitterling.

PHYSICAL CHARACTERISTICS
Small fish, body length usually shorter than 2.76 in (7 cm). Body very deep, oval-shaped, compressed laterally. Snout short and blunt. Mouth small, terminal. Barbels absent. Pharyngeal teeth compressed, in 1 row. Gill rakers 10–14. Dorsal fin moderate, with 3 unbranched, 10–12 branched rays; anal fin with 3 unbranched, 9–12 branched rays. Lateral line incomplete, with 2–6 scales. Olive green above, lower sides white. Males very colorful, with a red dot on the base of caudal fin; one horizontal blue stripe from below dorsal origin to caudal base; two transverse blue bands above shoulder area; and eyes that are reddish on their upper halves.

DISTRIBUTION
China and Vietnam. Has been introduced into Japan.

HABITAT
Shallow lakes, ponds, and streams. Prefers clear, slow-running water, especially when it includes aquatic plants.

BEHAVIOR
Normally found in small groups near the shore. In breeding season, males are territorial.

FEEDING ECOLOGY AND DIET
Pelagic feeder, taking zooplankton, algae, and fragmental plants.

REPRODUCTIVE BIOLOGY
Matures in the first year, spawns in the second year from April to May. During spawning, the male finds a mussel, then attracts a female to the site. They both swim around the mussel, and the female next lays eggs into the mussel with a tube (ovipositor). The male then releases sperm, which is carried by the current into the gill chamber of the mussel, where it fertilizes the eggs. The eggs hatch after one day, but the larvae stay in the gill chamber for about 20 days. When the air-bladders fill with air and the egg yolks are nearly gone, the larvae swim out of the gill chamber to live independently.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Bitterlings are interesting aquarium fishes because of their beautiful color and special breeding mode. They can be used to control mosquitos. In some places, they are used as indicators of environmental conditions, since they are sensitive to pollution. ◆

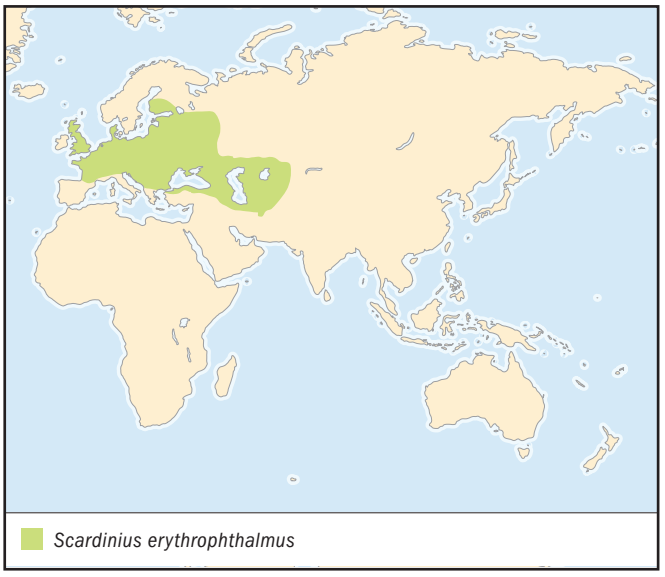
Rudd
Scardinius erythrophthalmus

FAMILY
Cyprinidae

TAXONOMY
Cyprinus erythrophthalmus Linnaeus, 1758, northern Europe.

OTHER COMMON NAMES
French: About, gardon rouge; German: Rotfeder; Spanish: Gardí; Russian: Krasnoperka.

PHYSICAL CHARACTERISTICS
Size moderate to large, maximum 20 in (51 cm) in total length. Body stocky and compressed. Mouth narrow, directed forward with the lower lip protruding. Belly strongly keeled between ventral fins and anus. Dorsal fin with 8–9 branched rays. Anal fin with 9–12 branched rays. Color brown-olive dorsally, sometimes with a brassy sheen; flanks brassy colored; belly silver-



white. Ventral, anal, and lower part of caudal fins are a brilliant golden-red. Males develop spawning tubercles.

DISTRIBUTION
Widespread in Europe and middle Asia in the basins of the North, Baltic, Black, Caspian (from Emba, Ural, and Volga to the rivers of the southern coast) and Aral Seas. Introduced to several countries.

HABITAT
Dwells mainly in waters with a soft bottom and strong plant growth, especially where there are reedy margins including lakes, rivers, marshlands, canals, and ponds.

BEHAVIOR
Shoaling species.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on invertebrates (including insect larvae and adults) and plants; particularly partial to insects from the water surface.

REPRODUCTIVE BIOLOGY
Matures after three to four years of age and spawns from mid-May to early June. The eggs adhere to water plants. The average rudd produces 108,000 to 211,000 eggs per kilogram of body weight. The young, which hatch after six to eight days, are no larger than a pinhead and spend the first part of their lives sheltering in shoals in the water margins. As the fry grow larger, they move out into deeper water and begin to feed on insects.

CONSERVATION STATUS
Although not listed by the IUCN, this species is threatened due to the introduction of other species.

SIGNIFICANCE TO HUMANS
Cultured as food in some countries; also used as bait for fishing. Although adults actively feed on macrophytes present in abundance in the environment, they are not an effective species for the biological clearing of weeds. Several countries report adverse ecological effects after introduction. ◆

No common name
Schizothorax prenanti

FAMILY
Cyprinidae

TAXONOMY
Oreinus prenanti Tchang, 1930, Omei Mountain, Szechuan, China.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Size moderate, often 5.9–7.87 in (15–20 cm) in body length. Body long, slightly compressed. Snout somewhat pointed. Mouth inferior, transverse. Sharp horny edge on lower jaw. Lower lip papillae. Barbels 2 pairs, length similar to eye diameter. Pharyngeal teeth are sharp and in three rows. Gill rakers 14–23. Dorsal fin short, 3 unbranched, 8 branched rays; anal fin 3 unbranched, 5 branched rays. Back of last unbranched fin ray weakly serrated. Scales small. Lateral line complete, with 90–109 scales. Two rows of large scales along the anus. Brown or blue-brown above, sometimes with black spots; belly light yellow. Fins also light yellow.

DISTRIBUTION
Upper reaches of the Yangtze River in China. However, the group Schizothoracin, adapted to the plateau environment, is mainly distributed in and around the Tibetan Plateau.

HABITAT
Lives on the bottom of large rivers. Normally stays in succession areas between swift- and slow-running waters. Prefers low temperatures.

BEHAVIOR
Populations of this species mainly stay in large rivers, but some migrate to tributaries with swift waters to spawn eggs.

FEEDING ECOLOGY AND DIET
Normally uses the sharp horny edge on its lower jaw to scrape algae. Its diet also includes insects.

REPRODUCTIVE BIOLOGY
Males mature in the third, females in the fourth year of life. Spawning occurs from March to April. Eggs are slightly adhesive, staying in apertures between stones to hatch. Fecundity varies from 20,000 to 40,000 eggs per individual.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Important food fish in local areas and very expensive. ◆

Tench
Tinca tinca

FAMILY
Cyprinidae

TAXONOMY
Cyprinus tinca Linnaeus, 1758, European lakes.

OTHER COMMON NAMES
French: Aiguillons, tanche; German: Alia.

PHYSICAL CHARACTERISTICS
Size moderate, normally 11.8 in (30 cm) in length, and rarely exceeding 23.6 (60 cm), and 3.97 lbs (1.8 kg) in weight; maximum age 14 years. Body robust, slightly compressed. Snout somewhat blunt. Mouth moderate, terminal, and oblique, with thick lips. Barbels 1 pair, very short. Pharyngeal teeth compressed, in 1 row. Gill rakers short, 12–14. Dorsal fin short, with 3 unbranched, 8 branched rays; anal fin with 3 unbranched, 7 branched rays. Scales small. Lateral line complete, with 100–105 scales. The caudal peduncle is characteristically deep and short. Skin thick and very slimy. Olive green above, dark green or almost black, with golden reflections, on ventral surface; the fins are always dark; eyes orange-red.

DISTRIBUTION
Eurasia, found throughout Europe to northwestern China.

HABITAT
Warm lakes and pools with weed and mud bottoms. It can tolerate low oxygen levels. In winter, this fish stays in the mud without feeding itself.

BEHAVIOR
Tench have limited home range. They are mostly solitary, occasionally occurring in small groups.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on bottom invertebrates and aquatic insect larvae. Young tench also feed on algae. Foraging is often active at dawn and dusk.

REPRODUCTIVE BIOLOGY
Matures in 3–5 years. Breeds in shallow water among dense vegetation, laying numerous sticky green eggs in the period from May to August. After hatching, the larvae remain attached to plants for several days. The fecundity is 300,000–400,000 eggs per kilogram of body weight.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Because its flesh is highly esteemed, the tench has considerable value, although it grows very slow. A golden color variety is a popular ornamental pond fish. ◆

Smallscale yellowfin
Xenocypris microlepis

FAMILY
Cyprinidae

TAXONOMY
Xenocypris microlepis Bleeker, 1871, Yangtze River, China.

OTHER COMMON NAMES
English: Fine-scaled yellowfin; Russian: Melkocheshuinyi zheltoper.

PHYSICAL CHARACTERISTICS
Size moderate, normally 4.67–8.8 in (11.9–22.4 cm) in body length; maximum 27.56 in (70 cm) in total length. Body long and compressed. Snout short and blunt. Mouth inferior, with sharp horny edge on the lower jaw. Barbels absent. Pharyngeal teeth in three rows; teeth in the main row compressed. Gill rakers 36–48. Dorsal fin short, with 3 unbranched, 7 branched rays; anal fin with 3 unbranched, 10–14 branched rays. Scales small. Lateral line complete, with 72–84 scales. Back gray-black, lower sides and belly silver-white. Dorsal fin dark; pectoral and ventral fins gray-white; anal and caudal fins orange-yellow.

DISTRIBUTION
East Asia from Amur River to Yellow River, Yangtze River, and Pearl River.

HABITAT
Large rivers and lakes. Prefers clear waters with vegetation.

BEHAVIOR
Congregates in schools in winter in deep waters. Moves to shore to catch food in spring. Migrates to upper reaches of rivers to breed.

FEEDING ECOLOGY AND DIET
Normally uses the sharp horny edge on its lower jaw to scrape algae on the bottom. Its diet includes algae, fragmental plants, and insect larvae.

REPRODUCTIVE BIOLOGY
Matures in the second year of life. Spawning occurs from April to June. When floods occur and the water level rises rapidly, mature fish swim against the current and spawn in areas with fast-flowing water and stony bottoms. Eggs are attached to stones and hatch there. Fecundity varies from 42,000 to 292,000 eggs.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Important food fish. Also used to keep fishery ponds clean.

Resources

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Huanzhang Liu, PhD

Cypriniformes II
(Loaches and relatives)

Class Actinopterygii
Order Cypriniformes
Number of families 4 of loaches and relatives

Photo: The tiger loach (*Botia dario*) is originally from India and Bangladesh. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Fossils of this order date as far back as the Oligocene (about 38 million years ago), and have been found in North America, Europe, and Asia.

Cypriniformes are in the superorder Ostariophysi, together with the Gonorhynchiformes, Characiformes, Siluriformes, and Gymnotiformes. This superorder is characterized by having a Webberian apparatus, i.e., the first four or five vertebrae, called ossicles, are modified and connect the inner ear with the swim bladder. Because of this, they can hear very well, which is an advantage in murky fresh waters. This may explain why this group has been so successful inland, while being absent from the marine environment. Another distinguishing characteristic of fishes in this superorder is the production of an alarm substance, a chemical released by their skin when damaged, which helps to warn conspecifics of possible danger.

There have been a number of classifications for the order Cypriniformes. The most commonly employed is that of Nelson (1994), in which the order is divided into two superfamilies. The first superfamily, Cyprinoidea, includes one family and eight subfamilies (Cyprininae, Gobioninae, Rasborinae [=Danioninae], Acheilognathinae, Leuciscinae, Cultinae, Alburninae, and Psilorhynchinae), and has a total of 210 genera and about 2,010 species. The second superfamily, Cobitoidea, includes four families: 1) Gyrinocheilidae, or algae eaters; 2) Catostomidae, or suckers, which includes three subfamilies (Ictiobinae, Cycleptinae, and Catostominae), 3) Cobitidae, or loaches, which includes two subfamilies (Cobitinae and Botiinae); and 4) Balitoridae (=Homalopteridae), or river loaches, which includes two subfamilies (Nemacheilinae and Balitorinae). The superfamily Cobitoidea has a total of about 70 genera and 690 subspecies. This is considered the most primitive within this order. The Cobitoidea represent the scope of this chapter.

Physical characteristics

From a morphological viewpoint, the Cobitoidea is not a very well-defined group (it could be said that it was largely put in place to differentiate all noncyprinid families of the Cypriniformes). Therefore, it is difficult to generalize in terms of major morphological characters. For example, the algae eaters, fishes in the family Gyrinocheilidae, lack pharyngeal teeth, while the number of teeth in fishes in other families is extremely variable, reflecting a great deal of ecological adaptations to different types of food. Sometimes the lateral line is complete, in other families it is incomplete or even absent. The algae eaters are further characterized by having a ventral mouth that has been modified for feeding on algae on hard substrate and by having inhalant and exhalant gill openings. The suckers (Catostomidae) have one row of 16 or more pharyngeal teeth and have four sets of chromosomes, a condition called tetraploidy. The loaches (Cobitidae) have an elongated body with a subterminal mouth and three to six pairs of barbels; the river loaches (Balitoridae) have three or more pairs of barbels near the mouth.

Distribution

Suckers occur in China, northeastern Siberia, and North America. The remaining families in this group are native to Eurasia and Africa, with some species having been introduced in other parts of the world. The algae eaters are found in parts of Southeast Asia and Borneo; loaches are found in Europe, Asia, and in Morocco (North Africa), with one species introduced in North America; the river loaches are found throughout most of Eurasia.

Habitat

Like the rest of the Cypriniformes, the families included in this chapter contain all freshwater fishes. They are mostly benthic, feeding and reproducing at or near the bottoms of

A sucker feeds on the sea floor. (Illustration by Wendy Baker)

rivers and streams, especially those that are medium to small in size. Several species are troglomorphic, i.e., blind and depigmented, and living in caves.

Behavior

Fishes in this group can be effective swimmers because of their need to adapt to fast-moving currents. Some members of the family Catostomidae use their ventral mouths to adhere to the bottom and thus avoid being swept away by currents. These fishes usually have a reduced swim bladder that prevents them from rising to the surface of the water (their least preferred habitat).

Clown loaches (*Botia macracanthus*) originate from Borneo and Sumatra, where they live in moving waters. (Photo by M. H. Sharp/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

There is a great variety of feeding habits and items in this group. Some fishes eat algae, others, such as those in the *Chasmistes* spp. in the family Catostomidae, are midwater planktivores, and most feed on aquatic insect larvae, worms, crustaceans, and detritus from the bottom. A large proportion of species in several families, including the Cyprinidae, have a mouth that is essentially ventral, which allows them to feed from the bottom. Others, such as some representatives of the family Balitoridae, have barbels around the mouth that help them locate food. These barbels can be so sensitive that they can sense an imminent thunderstorm. Members of this superfamily are preyed upon by other fishes and some aquatic reptiles and mammals.

Reproductive biology

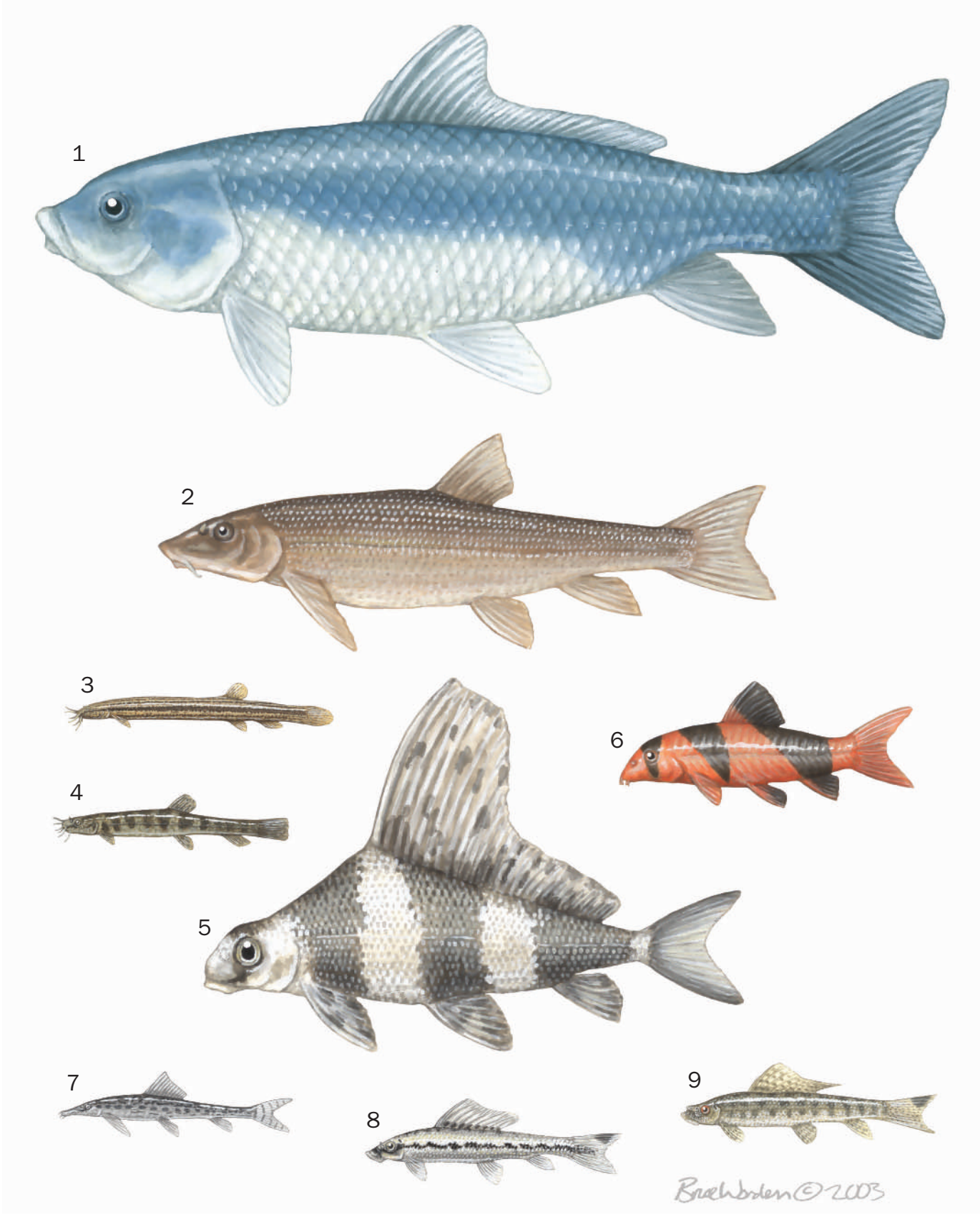
Some species, such as the longnose sucker (*Catostomus catostomus*), can engage in rather extensive upstream migrations prior to spawning. In many cases, two males compete for a single female, but not much is known about the genetic role played by each male. Some fishes, like the members of the family Catostomidae, are tetraploid, having four sets of chromosomes instead of the usual two, but only two sets are functional. The evolutionary meaning of this is unknown. Hybridization occurs among species in all the families, raising the question of the validity of the systematics.

Conservation status

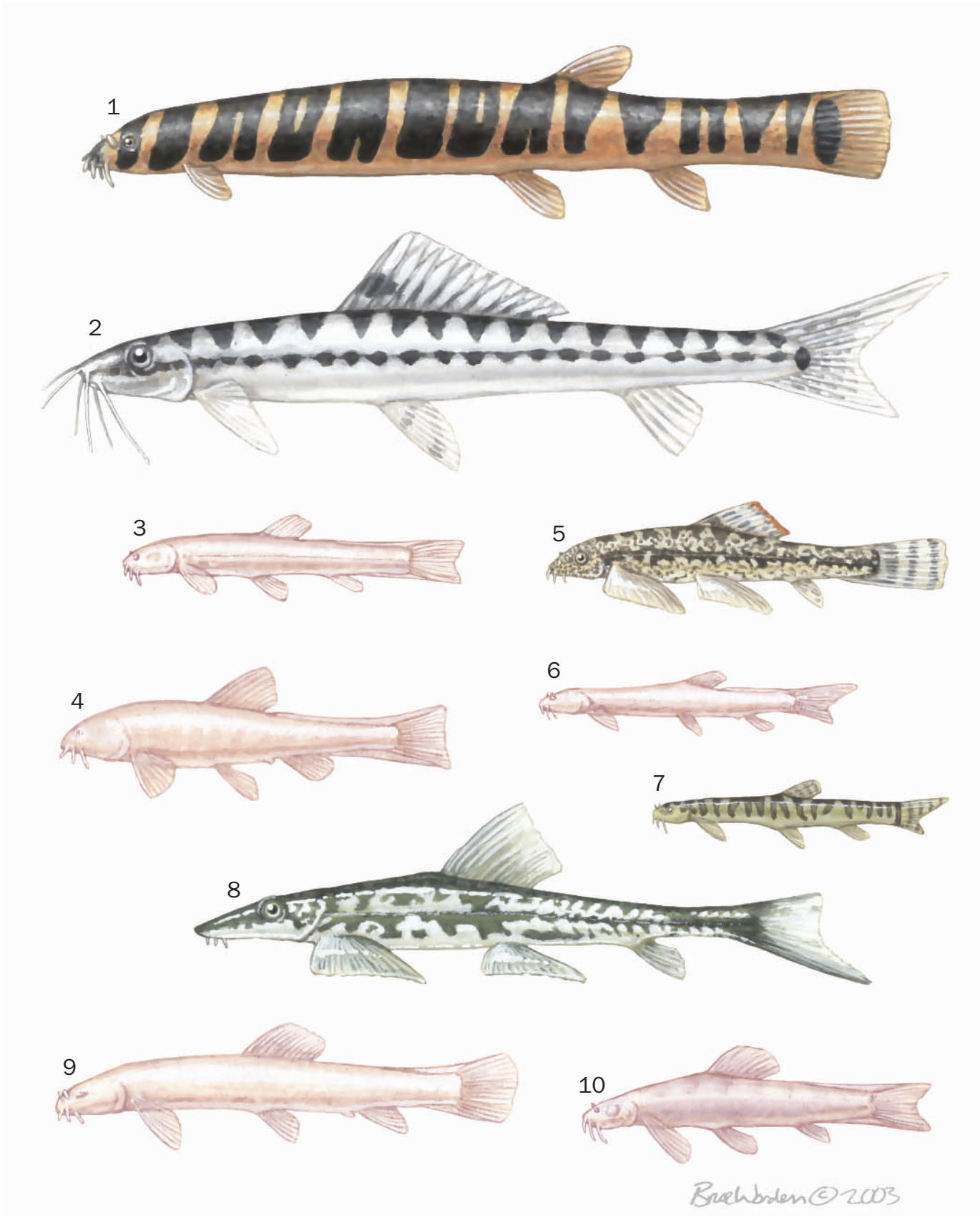
The IUCN Red List includes 65 species from these four families: two (*Chasmistes muriei* and *Moxostoma lacerum*) are Extinct; two are Critically Endangered; six are Endangered; 27 are Vulnerable; seven are Lower Risk/Near Threatened; one is Lower Risk/Conservation Dependent; and 20 are Data Deficient. Many of these species have a very restricted range and live in small streams that are very sensitive to pollution.

Significance to humans

Many species, particularly those in the Gyrinocheilidae, are commonly sold in pet shops because they are believed to be useful in keeping aquaria clean of algae. Others, such as the hillstream loaches of the family Balitoridae, are important as ecological indicators because of their sensibility to minor environmental change. A few species can occasionally be seen in fish markets, but since most are small, they are rarely of any commercial value. Others, such as those living in caves, are of scientific value because of their interest from an evolutionary standpoint.



1. Bigmouth buffalo (*Ictiobus cyprinellus*); 2. Longnose sucker (*Catostomus catostomus*); 3. Weatherfish (*Misgurnus fossilis*); 4. Stone loach (*Barbatula barbatula*); 5. Chinese sucker (*Myxocyprinus asiaticus*); 6. Clown loach (*Botia macracanthus*); 7. Horseface loach (*Acanthopsis choirorhynchus*); 8. Chinese algae eater (*Gyrinocheilus aymonieri*); 9. Spotted algae eater (*Gyrinocheilus pennocki*). (Illustration by Bruce Worden)



1. Coolie loach (*Pangio kuhlii*); 2. Arrow loach (*Nemacheilus masyae*); 3. Cavefish of Nam Lang (*Schistura oedipus*); 4. Kughitang blind loach (*Nemacheilus starostini*); 5. Chinese hillstream loach (*Pseudogastromyzon cheni*); 6. Blind loach (*Paracobitis smithi*); 7. Hillstream loach (*Nemacheilus evezardi*). 8. Anamia (*Annamia normani*); 9. Blind cave loach of Xiaao (*Protocobitis typhlops*); 10. Siju blind cavefish (*Schistura sijuensis*). (Illustration by Bruce Worden)

Species accounts

Anamia
Annamia normani

FAMILY
Balitoridae

TAXONOMY
Parhomaloptera normani Hora, 1931, Annam.

OTHER COMMON NAMES
Laotian: Pa tit hin.

PHYSICAL CHARACTERISTICS
Standard length 3.07 in (7.8 cm). Characterized by a flat belly, a small, horseshoe shaped mouth located far from the tip of the snout. Only one simple ray in the pelvic and pectoral fins.

DISTRIBUTION
Mekong River basin.

HABITAT
Steeped streams and rivers, on shallow and fast waters, prefers rocky bottoms.

BEHAVIOR
Swims slowly over the bottom.

FEEDING ECOLOGY AND DIET
Feeds on small benthic animals, primarily insect larvae.

REPRODUCTIVE BIOLOGY
No information available.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Stone loach
Barbatula barbatula

FAMILY
Balitoridae

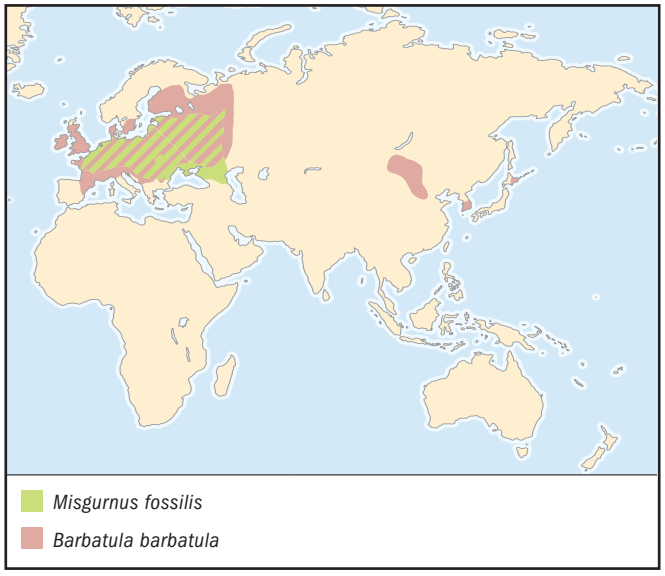
TAXONOMY
Cobitis barbatula Linnaeus, 1758, Europe. May be the same species as *Nemacheilus toni*, the Siberian stone loach.

OTHER COMMON NAMES
English: European stone loach, groundling; French: Loche franche; German: Schmerle; Spanish: Gobio de río.

PHYSICAL CHARACTERISTICS
Maximum total length 8.3 in (21 cm); maximum weight 0.4 lb (200 g). Fishes in this species have an elongated, slender body that is somewhat flattened in the first half but laterally compressed in the second half. The species is characterized by three pairs of mouth barbels and no erectile spine below the eye.

DISTRIBUTION
Very common from Ireland (where it was introduced) throughout Europe (except in the Italian and Iberian peninsula), and Asia to China. There are reports of this species from Siberia and Japan, but the taxonomy of the specimens collected there is not clear.

HABITAT
Shallow, fast-flowing creeks with gravel bottoms, as well as in shallow areas of clear lakes.



BEHAVIOR
Usually swims near the bottom. Mostly active at dusk and night, shelters underneath rocks or burrows in sand.

FEEDING ECOLOGY AND DIET
Feeds on small crustaceans, insect larvae, and benthic invertebrates. They are fed upon by birds.

REPRODUCTIVE BIOLOGY
Breeds from April to June, spawning more than once. Deposits eggs among rocks and aquatic plants.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
These fishes are sensitive to pollution and low oxygen levels, so their presence in a river can be taken as an indication of good water quality. ◆

Hillstream loach
Nemacheilus evezardi

FAMILY
Balitoridae

TAXONOMY
Nemacheilus evezardi Day, 1872, "A cave in India." Kottelat (1990) changed the generic status of this species to *Indoreonectes*, but without explanation. Singh and Yazdani (1993) gave it the name of *Oreonectes evezardi*.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum total length 2 in (3.8 cm). Characterized by small eyes and minute scales. They are mostly depigmented.

DISTRIBUTION
Kotumsar Cave (18°52'09"N, 81°56'05"E) of the Bastar District, Madhya Pradesh State, India.

HABITAT
The cave in which they occur is at 1,837 ft (560 m) above sea level and is subject to frequent flooding during the monsoon season.

BEHAVIOR
They have a low oxygen consumption, but despite living in a cave, they still exhibit circadian (day-to-day) and circannual (year-to-year) rhythmicity, which suggests that the cave population recently (in terms of evolution) invaded the cave environment.

FEEDING ECOLOGY AND DIET
Little is known.

REPRODUCTIVE BIOLOGY
Little is known.

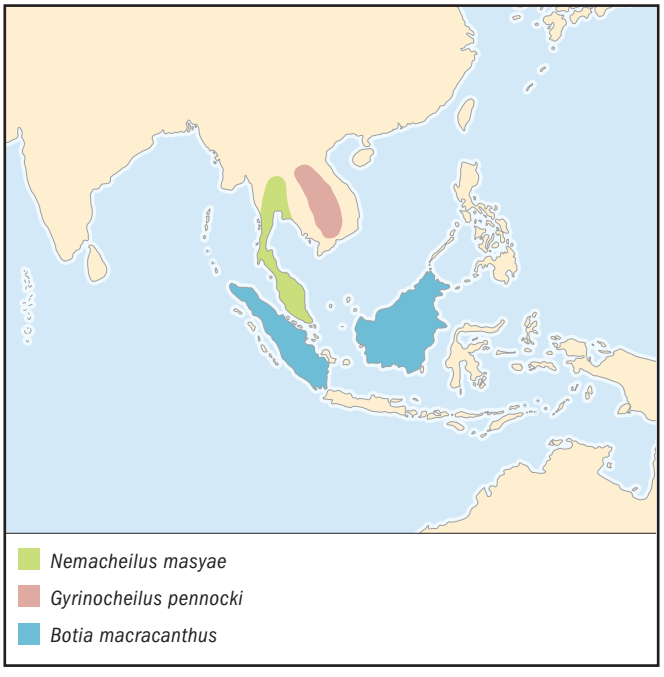
CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Of scientific value because of its adaptation to its cave environment. ◆

Arrow loach
Nemacheilus masyae

FAMILY
Balitoridae

TAXONOMY
Nemacheilus masyae Smith, 1933, Siam.



OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Standard length 5.31 in (13.5 cm). What separates this species from others in the Nemacheilinae in Indochina is the color pattern, which consists of a light background with 14–18 dark blotches along the sides and 12–17 dark saddles along the back. They also have a black spot at the posterior extremity of the lateral line and a black spot on the anterior dorsal rays at about one-fourth of ray length. They have a slender body with the eyes situated more on the top of the head.

DISTRIBUTION
Western Malaysia, Peninsular Thailand, and the Meklong basin, as well as in parts of the Mae Nam Chao Phraya basin.

HABITAT
Mostly forest streams with clear or more turbid waters, in depths of 6.6 ft (2 m) or less in rivers and streams with a moderate current and muddy to sandy bottoms.

BEHAVIOR
Adults can be aggressive toward conspecifics.

FEEDING ECOLOGY AND DIET
Feeds on insect larvae and aquatic invertebrates.

REPRODUCTIVE BIOLOGY
No information is available.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Found in the aquarium trade. ◆

Kughitang blind loach
Nemacheilus starostini

FAMILY
Balitoridae

TAXONOMY
Noemacheilus (Troglobitis) starostini Parin, 1983, Turkmenistan. Weber (2000) gave it the name of *Paracobitis starostini.*

OTHER COMMON NAMES
English: Starostin's loach.

PHYSICAL CHARACTERISTICS
Has no externally visible eyes, no pigmentation, no scales, and no swim bladder, all convergent features among many hypogean species.

DISTRIBUTION
Several sinkholes (ca. 37°55' N, 66°23' E) of the Khrebet Kughitang (mountains), in the Chardzhou province of the Republic of Turkmenistan.

HABITAT
Found in a sinkhole about 62 ft (19 m) deep with a seasonally fluctuating water level. A large portion of the pool is exposed to light part of the time. The pool is connected to an underwater stream. Up to 40 fish can be observed at a time in the pool.

BEHAVIOR
No information is available.

FEEDING ECOLOGY AND DIET
Feeds on insect larvae and small benthic crustaceans.

REPRODUCTIVE BIOLOGY
Other than reproducing via external fertilization, nothing else is known.

CONSERVATION STATUS
Classified as Vulnerable by the IUCN because of the susceptibility of their narrow habitat to underground pollution.

SIGNIFICANCE TO HUMANS
Of scientific interest because of their adaptation to the hypogean environment. ◆

Blind loach
Paracobitis smithi

FAMILY
Balitoridae

TAXONOMY
Noemacheilus smithi Greenwood, 1976, Iran.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Lacks externally visible eyes, pigmentation, and scales.

DISTRIBUTION
Found exclusively in a natural well in an oasis at Kaaje-Ru (33°05' N, 48°36' E), in Ab-i-Serum Valley near Tang-e-haft railway station, at the Zagros Mountains, in the Lorestan (Khorramabad) province of Iran.

HABITAT
Occurs in a well-like water resurgence that seems to be the result of a collapsed subterranean system. This is probably part of a larger, but complex, narrow, and inaccessible network of underground waters. This species is syntopic with *Iranocypris typhlops*, that is, it shares the same habitat within the same geographical range.

BEHAVIOR
No information is available.

FEEDING ECOLOGY AND DIET
Most likely feeds on small invertebrates and/or detritus.

REPRODUCTIVE BIOLOGY
Nothing is known about its reproductive habits except that fertilization is external.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Chinese hillstream loach
Pseudogastromyzon cheni

FAMILY
Balitoridae

TAXONOMY
Pseudogastromyzon cheni Liang, 1942, Fukien, China.

OTHER COMMON NAMES
German: Chinesischer Flossensauger.

PHYSICAL CHARACTERISTICS
Maximum total length at least 2 in (5 cm). They have fins as modified suckers, and their mouths are below their bodies, like saltwater rays.

DISTRIBUTION
Inland waters of China.

HABITAT
Benthic; prefers waters of 68–77°F (20–25°C).

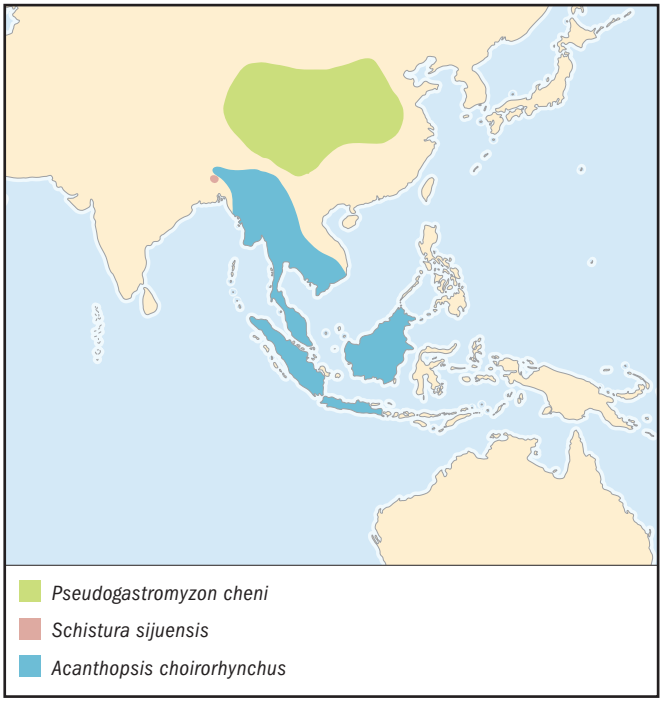
BEHAVIOR
Not aggressive, and thus do not defend well against other fishes trying to take away territory.

FEEDING ECOLOGY AND DIET
Feeds on a variety of sources, including algae, plants, and invertebrates.

REPRODUCTIVE BIOLOGY
Breeds in pits built under rocks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Common in the aquarium trade. ◆



Cavefish of Nam Lang
Schistura oedipus

FAMILY
Balitoridae

TAXONOMY
Nemacheilus oedipus Kottelat, 1988, Tham Nam Lang, Thailand.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Standard length 2.2 in (5.4 cm). It is microphthalmic, almost totally depigmented, and has embedded scales. Also characterized by a forked caudal fin.

DISTRIBUTION
Thailand, in the Mae Hong Son Province in the Tham (cave) Nam Lang (19°31' N, 98°09' E).

HABITAT
Has been found in an outflow of a cave with a stream that is probably part of Nam Lang, part of a karstic endoreic basin, usually on muddy bottoms.

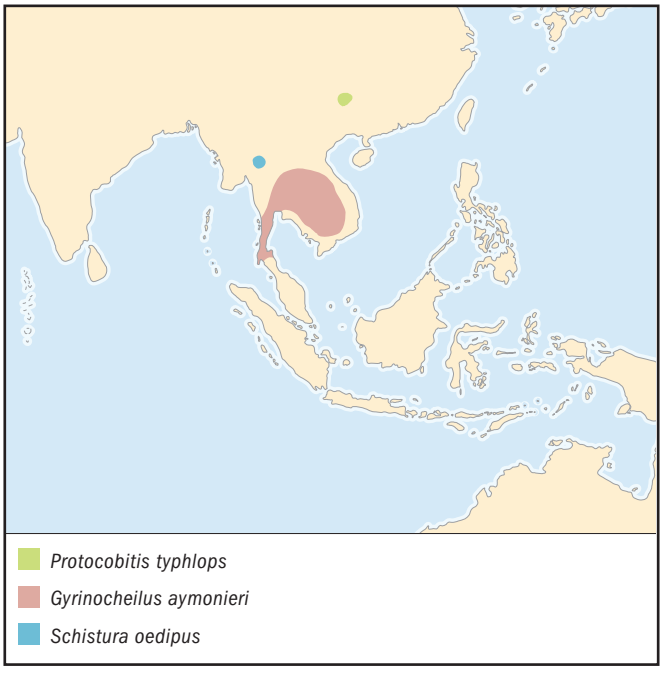
BEHAVIOR
Scotophilic (moves away from light) and may have some residual "biological clock" (day/night rhythmicity).

FEEDING ECOLOGY AND DIET
Feeds on insects and roundworms.

REPRODUCTIVE BIOLOGY
Scatters eggs on the bottom.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
No commercial value; of scientific interest. ◆



Siju blind cavefish
Schistura sijuensis

FAMILY
Balitoridae

TAXONOMY
Noemacheilus sijuensis Menon, 1987, Siju Cave, India. *Noemacheilus Mesonoemachilus sijuensis* appears on the plate caption of the original description. Pillai and Yazdani (1977) refer to this fish as *Nemacheilus multifasciatus*. However, Talwar and Jhingran (1991) consider these two separate species, and when referring to *N. multifasciatus* make no mention of it being found in a cave.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Standard length 2 in (5.1 cm). The first cave individuals belonging to this species may have been reported by Hora (1924), who described three specimens as "*Nemacheilus*" sp. from the "Siju Cave, Assam, India." One specimen caught within 115 ft (35 m) of the cave mouth showed coloration comparable to the epigean (not cave-restricted) forms. Two others netted about 1,800 ft (550 m) from the entrance of the cave were paler in color, had reduced scales and reduced eyes.

DISTRIBUTION
Siju Cave (ca. 25°25' N, 90°30' E), Garo Hills, Meghalaya, India.

HABITAT
Found only in caves.

BEHAVIOR
No information is available.

FEEDING ECOLOGY AND DIET
Nothing known.

REPRODUCTIVE BIOLOGY
No information is available.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

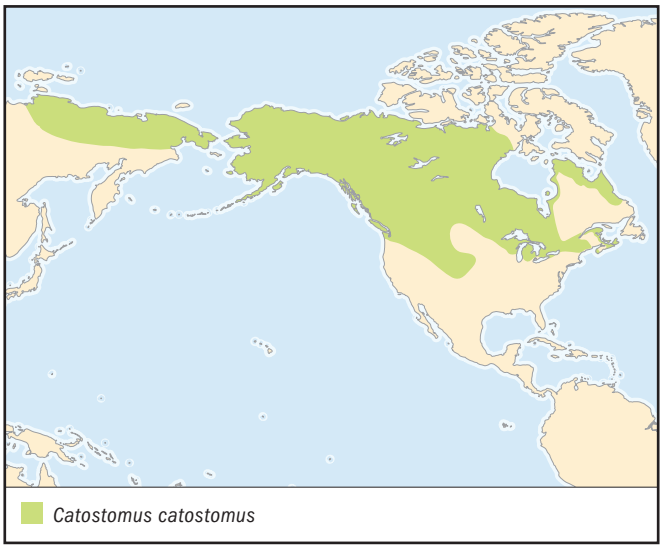
SIGNIFICANCE TO HUMANS
Of scientific interest because of their adaptations to the cave environment. ◆

Longnose sucker
Catostomus catostomus

FAMILY
Catostomidae

TAXONOMY
Cyprinus catostomus Forster, 1773, tributaries of the Hudson's Bay.

OTHER COMMON NAMES
English: Black sucker, red-sided sucker; French: Meunier rouge; German: Maulbiden-Saugdöbel.



PHYSICAL CHARACTERISTICS
Maximum total length 21.2 in (64 cm); maximum weight 7.3 lb (3.3 kg). This species is characterized by a ventrally placed sucking mouth with thick papillose lips. The fishes also have an inconspicuous but complete lateral line, short gill rakers, and slightly rounded caudal tips. The color varies with age and reproductive state: young fishes are usually dark gray with small black spots; adults may be reddish brown, dark brassy green or black above, paler on the lower sides, with the ventral parts white. Breeding males are usually dark above with a brilliant reddish stripe along each side, and show prominent tubercles on the rays of the anal and caudal fins and also on the head. Breeding females are greenish gold to copper, with a less brilliant red stripe.

DISTRIBUTION
North America throughout most of Canada and Alaska; and in the drainages of the Delaware River (New York State, United States), Columbia River, upper Monongahela River (Maryland and West Virginia, United States), and Missouri River (south to Nebraska and Colorado, United States), and in the Great Lakes basin and the Arctic basin of Siberia (Russia).

HABITAT
Clear, cold, deep waters of lakes and tributary streams; occasionally brackish water in the Arctic.

BEHAVIOR
Moves from lakes into inlet streams or from slow, deep pools into shallow, gravel-bottomed portions of streams to spawn.

FEEDING ECOLOGY AND DIET
Feeds on benthic invertebrates. Young are preyed upon by other fishes and fish-eating birds; adults in spawning streams are eaten by otters, bears, ospreys, and eagles.

REPRODUCTIVE BIOLOGY
Spawning takes place during daytime over coarse gravel bottoms. Males, which do not engage in nest-building behavior, stay close to the bottom of fast-moving streams. Females keep themselves to the banks of still water from which they swim to the areas where the males are. Females are soon escorted by up to five (but usually two) males to the center of the stream. Males then engage in a ritual that lasts up to six seconds, either clasping the females with their pelvic fins or vibrating with

their anal fins against her. Egg deposition occurs at this time. After this, males and females return to their place of origin.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Utilized as food for humans or dogs. ◆

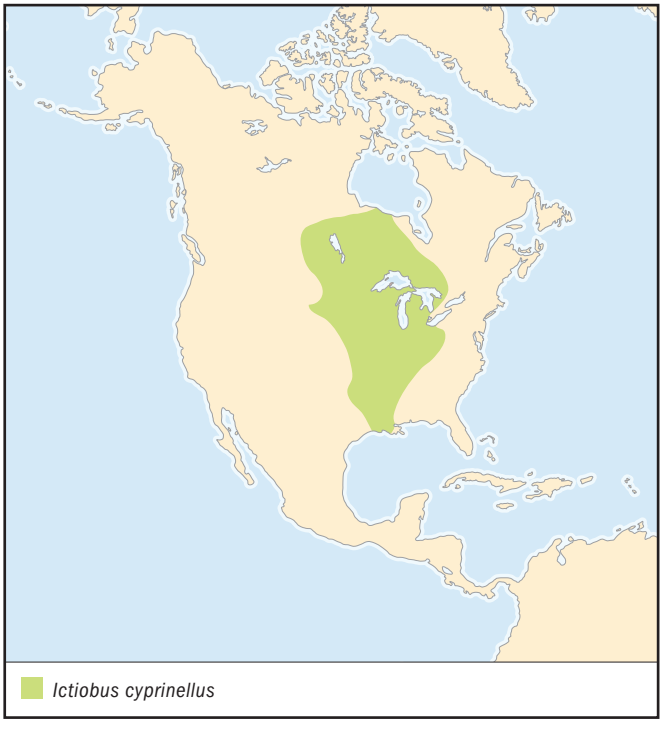
Bigmouth buffalo
Ictiobus cyprinellus

FAMILY
Catostomidae

TAXONOMY
Sclerognathus cyprinella Valenciennes, 1844, near New Orleans, Lake Pontchartrain, Louisiana, United States.

OTHER COMMON NAMES
English: Bigmouth buffalo, bullhead buffalo, common buffalofish; Romanian: Buffalo cu gura mare.

PHYSICAL CHARACTERISTICS
Maximum total length 48.4 in (123 cm); maximum weight 70.3 lb (31.9 kg). Characterized by a large, robust, and somewhat deep body. They are dorsally lighter in color on the rest of the body. Other characteristics include an anteriorly curved ventral line, a bluntly rounded snout, and a terminate mouth with thin lips, of which the lower one is striated. They have a total of approximately 165 short pharyngeal teeth. The dorsal fin is sickle shaped, with between 24 and 32 rays; the anal fin rays have between 8 and 10 rays. The lateral line is complete, with between 34 and 39 scales.



DISTRIBUTION
North America: in the Hudson Bay (Nelson River drainage), lower Great Lakes, and Mississippi River basins from Ontario to Saskatchewan in Canada, and from Montana south to Louisiana in the United States. Successfully introduced to California, Arizona, Virginia, and North Carolina, in the United States; and in Uzbekistan, the Jordan River, Romania, and Cuba.

HABITAT
Occurs in a great variety of habitats, including still waters such as ponds, pools, impoundments, and floodplain lakes with shallow waters, as well as large rivers, main channels, and backwaters of small to large rivers.

BEHAVIOR
Usually forms schools.

FEEDING ECOLOGY AND DIET
Benthic feeders that feed on copepods, caldocerans, bottom plants, aquatic insects, mollusks, small fishes, and fish eggs. They are preyed upon by northern pikes, black bullheads, and walleyes.

REPRODUCTIVE BIOLOGY
Usually mature at age three. Spawning often occurs between April and May (at least in North America), when water temperatures rise suddenly and remain between 60.1 and 65°F (15.6 and 18.3°C). Adults migrate into the shallow bays and inlets of lakes or into sloughs and flooded marshes of large rivers. At times they swim over the top of one another as they move through small, shallow inlets into the sloughs. They can spawn at any time of the day over low, sparse vegetation, rocks, or even mud, but the water must be clear. Spawning takes place in groups of one female surrounded by two to four males. During spawning, the female swims, making huge ripples and hitting the surface with her tail. Then she sinks to the bottom and releases her eggs. The males then push in all around in order to move into a position to fertilize the eggs. Then they make a tremendous rush, causing the water to foam. The whole spawning process is very noisy and splashy. Depending on her size, a single female can lay 100,000–750,000 eggs. The eggs adhere to any object they contact. Hatching occurs after 9 or 10 days and the larvae remain in shallow water to feed.

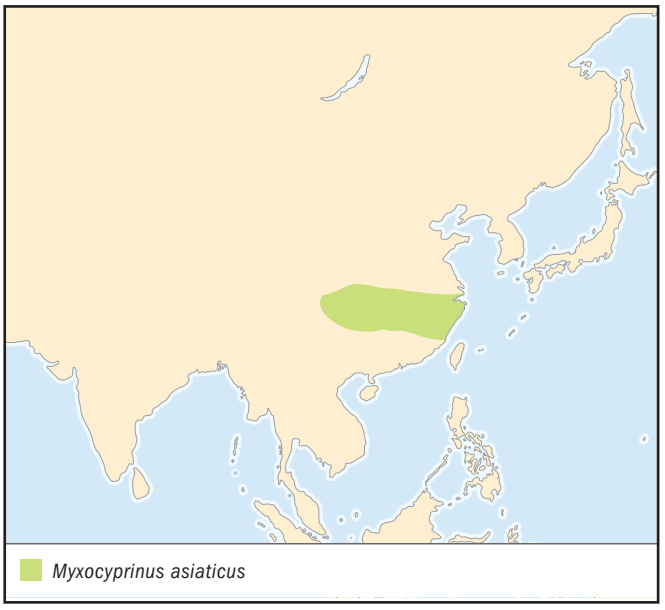
CONSERVATION STATUS
Not listed by the IUCN, but not as abundant as in the early twentieth century. This decline was due to overexploitation for commercial purposes.

SIGNIFICANCE TO HUMANS
Important food fishes; this species has been artificially propagated. Fishes in this species may compete with native minnows and suckers, as well as with juvenile sport fishes, for food and space. The meat is nutritious; the taste of the flesh is considered to be inferior to that of the flesh of the catfish but superior to that of carp. ◆

Chinese sucker
Myxocyprinus asiaticus

FAMILY
Catostomidae

TAXONOMY
Carpiodes asiaticus Bleeker, 1865, China.



OTHER COMMON NAMES
English: High fin banded shark, freshwater batfish; German: Wimpelkarpfen; Finnish: Kiinanimukarppi.

PHYSICAL CHARACTERISTICS
At least 23.6 in (60 cm) in length. The most important characteristic of this species is its unusual deep, flat body, that elongates somewhat as the fish grows.

DISTRIBUTION
Upper and middle tributaries of the Yangtze River basin in China.

HABITAT
Unlike most other Catostomidae, they occur in large (and cool) rivers of temperate areas.

BEHAVIOR
Forms schools.

FEEDING ECOLOGY AND DIET
Feeds on algae and plants (at least under captive conditions).

REPRODUCTIVE BIOLOGY
Spawns in small groups in quiet waters.

CONSERVATION STATUS
Not listed by the IUCN, but considered endangered in China due to habitat destruction.

SIGNIFICANCE TO HUMANS
Sold in the aquarium trade. Prior to construction of Gezhouba Dam on the Yangtze River, the fish was a popular food fish in Sichuan Province. After construction of the dam, catches declined dramatically and attempts to reestablish reproducing populations have not been successful. Small breeding populations remain below the dam. ◆

Horseface loach
Acanthopsis choirorhynchus

FAMILY
Cobitidae

TAXONOMY
Cobitis choirorhynchus Bleeker, 1854, Sumatra.

OTHER COMMON NAMES
English: Banana fish, longnose loach; German: Lanstirnschmerle; Laotian: Pa it; Malay: Jeler; Spanish: Locha de hocico largo; Thai: Pla sai, pla chon sai; Vietnamese: Cá chia voi.

PHYSICAL CHARACTERISTICS
Maximum total length 12 in (30 cm). Mimetic fishes with a great ability to change coloration to appear similar to almost all natural backgrounds.

DISTRIBUTION
India, Myanmar, Thailand, Malaya, Indonesia (Sumatra and Java), Borneo, and Vietnam (basinwide mainstream of the lower Mekong River).

HABITAT
Demersal, freshwater fishes found mostly in swift, clear streams, as well as in large rivers and flooded fields. Burrows in sandy or gravelly bottoms.

BEHAVIOR
Nocturnal; likes to bury during the day. Not aggressive.

FEEDING ECOLOGY AND DIET
Omnivorous.

REPRODUCTIVE BIOLOGY
Oviparous; lays eggs underneath small rocks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Common in the aquarium trade. ◆

Clown loach
Botia macracanthus

FAMILY
Cobitidae

TAXONOMY
Cobitis macracanthus Bleeker, 1852, Sumatra. Sometimes known as *Botia macracantha.*

OTHER COMMON NAMES
English: Tiger botia; German: Prachtsschmerle; Malay: Ikan macan.

PHYSICAL CHARACTERISTICS
Maximum total length 12 in (30 cm). They have a rather deep body, which is orange with three black stripes. A fourth stripe is sometimes present. The caudal fin is forked. Males have a larger tail that hooks inward rather than pointing straight out from the body. Females are smaller and more slender.

DISTRIBUTION
Sumatra and Borneo in Indonesia. It has been introduced in Thailand and the Philippines, but the success of such introductions is unknown.

HABITAT
Demersal freshwater fishes that prefer streams.

BEHAVIOR
Nonaggressive; spends most of the time at the bottom swimming or stationary among vegetation.

FEEDING ECOLOGY AND DIET
Feeds on benthic algae and weeds, benthic crustaceans, and worms.

REPRODUCTIVE BIOLOGY
Breeds only at the beginning of the rainy season and does so in fast-flowing rivers. Rarely breeds under captive conditions, which is why so little is known about their reproductive behavior.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular aquarium fishes; sometimes consumed as food. ◆

Weatherfish
Misgurnus fossilis

FAMILY
Cobitidae

TAXONOMY
Cobitis fossilis Linnaeus, 1758, Europe.

OTHER COMMON NAMES
French: Loche d'étang; German: Europäischer Schlammpeitzger; Czech: Cik; Finnish: Mutakala; Romanian: Chiscar.

PHYSICAL CHARACTERISTICS
Maximum total length 12 in (30 cm). Very elongated bodies. The total number of spines per fins is dorsal: three; dorsal (soft rays): five to six; pectoral: one; pectoral (soft rays): eight; anal: three; anal (soft rays): five; and caudal: 14. They have 16–17 gill rakers. Total number of vertebrae 49–50.

DISTRIBUTION
Central and eastern Europe, from France to Russia; successfully introduced in Spain and Croatia.

HABITAT
Mainly the lower reaches of slow-flowing rivers, in still pools, over sandy bottoms.

BEHAVIOR
Although it is a facultative air-breather, spends most of the day buried in the sand and is considered nocturnal. Not aggressive.

FEEDING ECOLOGY AND DIET
Feeds on small invertebrates, mostly insect larvae and mollusks.

REPRODUCTIVE BIOLOGY
Reaches sexual maturity when two years old. Spawns between April and June. The developing eggs and embryos of this species interact with each other in such a manner that the embryos of more advanced stages are in most cases suppressing the development of younger ones.

CONSERVATION STATUS
Classified as Lower Risk/Near Threatened by the IUCN. Also listed in the Appendix III of the Bern Convention.

SIGNIFICANCE TO HUMANS
Valuable as an ecological indicator because of its sensitivity to pollutants accumulated in sediments. ◆

Coolie loach
Pangio kuhlii

FAMILY
Cobitidae

TAXONOMY
Cobitis kuhlii Valenciennes, 1846, Malay Peninsula. It may represent a species complex (Kottelat et al., 1993); commonly used synonyms include *Acanthophthalmus kuhli*, *A. semicinctus*, and *Pangio semicincta*.

OTHER COMMON NAMES
English: Leopard loach, slimy loach; German: Halbgebändertes Dornauge; Spanish: Culebrita.

PHYSICAL CHARACTERISTICS
Maximum total length 4.7 in (12.0 cm). This species is characterized by an elongated and scaleless body. The basic color is dark brick red, with six to ten lighter, irregular stripes running down the body. They also have a dark and large quadrangular blotch occupying the proximal half of the caudal fin. All fins are small and transparent.

DISTRIBUTION
Indonesia in West Java, Sumatra, Kalimantan Timur and Kalimantan Barat in Borneo, and the Malay Peninsula at least as far north as Phangnga. Introduced in the Philippines with unknown success.

HABITAT
Sandy bottoms of clear, fresh waters.

BEHAVIOR
Solitary and nocturnal, they like to burrow in fine sand.

FEEDING ECOLOGY AND DIET
Omnivorous bottom feeders.

REPRODUCTIVE BIOLOGY
Scatters adhesive, floating green eggs that attach to floating vegetation. Growth rate constant; reaches maturity between 2.44 and 3.22 in (6.2–8.2 cm) in length.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
They can be found in the aquarium trade. ◆

Blind cave loach of Xiaao
Protocobitis typhlops

FAMILY
Cobitidae

TAXONOMY
Protocobitis typhlops Yang Chen, and Lan, 1994, cave in Guangxi, Duan County, China.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Adult length up to 1.77 (5.4 cm). These fishes are depigmented, and lack visible eyes and a lateral line. Scales are rudimentary and only along the midline of the sides of the body. Also lack a bony swim-bladder capsule, which may be a primitive characteristic.

DISTRIBUTION
Asia in a cave located in the province of Guangxi, Duan county, near the town of Xiaao (24°15'N, 107°05' E), China.

HABITAT
The cave where they live is 689 ft (210 m) above sea level.

BEHAVIOR
Swims slowly near the bottom.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Classified as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Of scientific value because of its adaptations to the cave environment. ◆

Chinese algae eater
Gyrinocheilus aymonieri

FAMILY
Gyrinocheilidae

TAXONOMY
Psilorhynchus aymonieri Tirant, 1883, mountains of Samrong-Tong, Cambodia.

OTHER COMMON NAMES
English: Sucker loach; German: Siamesische Saugschmerle; Spanish: Pez ventosa, chupa-algas; Khmer: Chun chuok dai; Thai: Pla e-dood.

PHYSICAL CHARACTERISTICS
Standard length 11.02 in (28 cm). This species, like other members of the family, is characterized by a ventral mouth modified for sucking. They also have nine branched dorsal rays, 36 to 43 lateral line scales, no dark spots on the pelvic and anal fins, a small dark spot always present behind the spiracle, and sometimes tiny tubercles on the side of the head and large tubercles on the snout. It has a long black stripe laterally and a pair of bright blue spots, one underneath the head and one on top of the anal fin.

DISTRIBUTION
Asia, specifically the Mekong, Chao Phraya, Meklong, and Xe Bangfai basins, and also the northern Malay Peninsula.

HABITAT
Solid surfaces in flowing waters of medium to large-sized rivers and flooded fields.

BEHAVIOR
Under fast-flowing current conditions, holds on to fixed objects with its suckerlike mouth. Has a small spiracle that operates as an inhalant opening for absorbing oxygen from the water. Because of the small size of the gill cavity, lives in highly oxygenated waters with a breathing rate of up to 240 times per minute. Peaceful as juveniles, but become territorial and aggressive as adults.

FEEDING ECOLOGY AND DIET
Almost exclusively herbivorous; feeds mostly on algae but occasionally consumes phytoplankton, zooplankton, and insect larvae.

REPRODUCTIVE BIOLOGY
No information is available.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular among aquarists because of their reputed ability to clean algae in home aquaria. Large individuals are sold in fish markets of Southeast Asia. Small ones are used to make *praboc*, a fermented fish paste consumed mostly in Cambodia. ◆

Spotted algae eater
Gyrinocheilus pennocki

FAMILY
Gyrinocheilidae

TAXONOMY
Gyrinocheilops pennocki Fowler, 1937, Siam.

OTHER COMMON NAMES
Khmer: Trey smok; Laotian: Ko, pa wa.

PHYSICAL CHARACTERISTICS
Standard length 11 in (28.0 cm). They are characterized by having large tubercles on sides of head (in larger specimens), 10 branched dorsal rays, with all fins strongly spotted, and a dark spot just behind the spiracle. Brownish coloration, darker dorsally. They have approximately 12 diffused, vertical, dark stripes laterally.

DISTRIBUTION
Mekong basin.

HABITAT
Solid surfaces of the bottom of fast-moving waters.

BEHAVIOR
No information is available.

FEEDING ECOLOGY AND DIET
Feeds mostly on algae, but occasionally on aquatic plants, zooplankton, and small invertebrates.

REPRODUCTIVE BIOLOGY
No information is available.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Large individuals are occasionally sold in fish markets. ◆

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Aldemaro Romero, PhD

Characiformes
(Characins)

Class Actinopterygii
Order Characiformes
Number of families 11

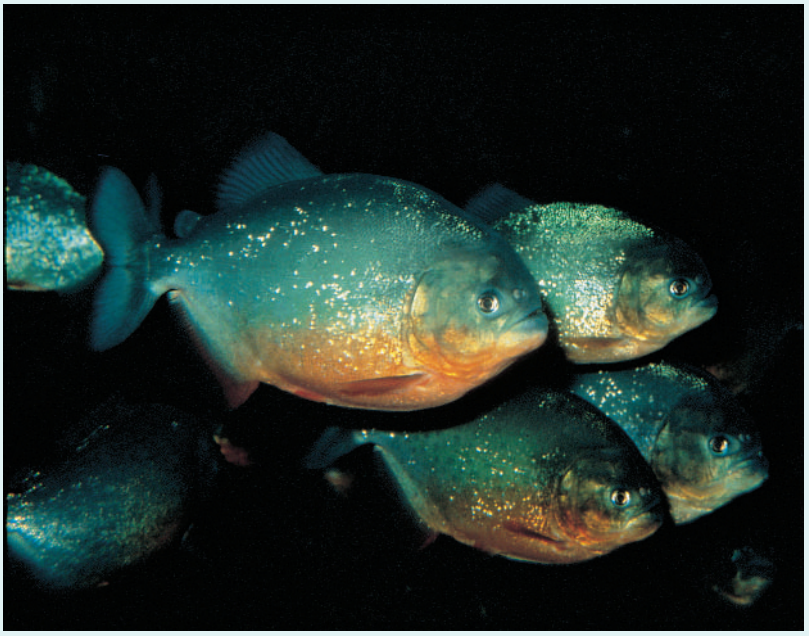


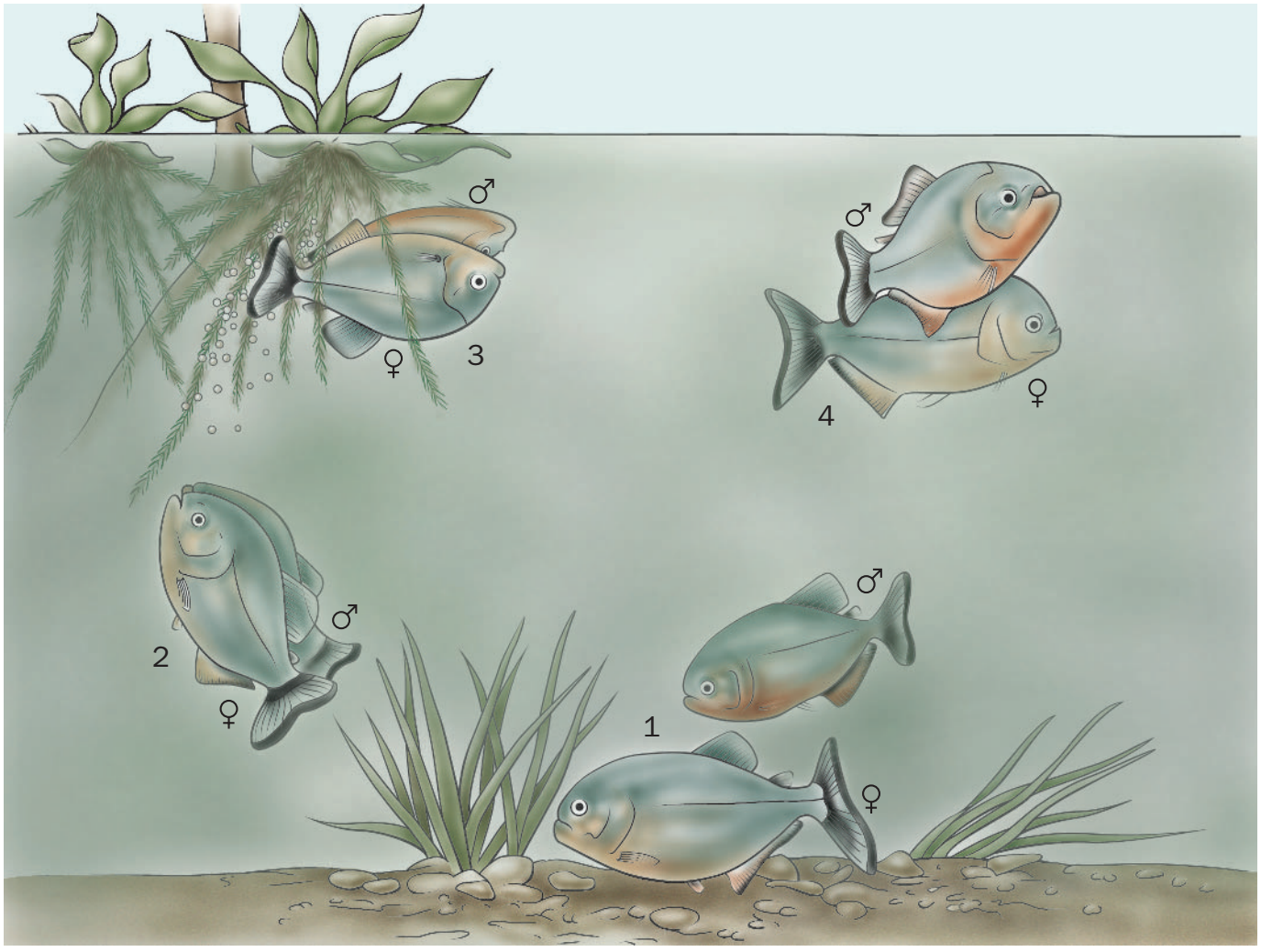
Photo: Red-bellied piranhas (*Pygocentrus nattereri*) in the Amazon. Red-bellied piranhas always face the same direction when they hunt together. (Photo by Davis M. Schleser/Nature's Images/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Characiformes are members of the superorder Ostariophysi, which contains nearly three-quarters of all freshwater fishes in the world. Characiformes possess several specialized adaptations, common to most Ostariophysi, which enable them to thrive in freshwater environments. One specialized anatomical feature is the presence of the Weberian apparatus, a linkage of bones called ossicles, derived from the vertebrae immediately following the skull, that connect the inner ear and the swim bladder; this structure improves the hearing ability of the fishes. Another evolved characteristic is the production of *Schreckstoff*, an alarm pheromone released into the water by an injured fish that triggers an escape response in other members of the species. Certain Characiformes, such as blind cavefish, do not produce these pheromones, as such a substance would not enhance a blind fish's ability to escape predators. Other species do not respond to the presence of the pheromones; for example, many characins preyed on by piranhas produce *Schreckstoff*, but piranhas do not flee when feeding on these species. Finally, the presence of a moveable upper jaw confers a feeding advantage to Characiformes. In some species, the jaw is protrusible, enabling the fishes to use suction pressure to capture prey.

Lineages of Characiformes date back more than 100 million years. Morphological and genetic evidence suggests that much of the species diversity of this group likely developed prior to the time when Africa and South America split into separate continents. The classification of the Characiformes into families has proven complex and controversial. The taxonomic relationships have been revised considerably in the last 30 years, and the classifications continue to change as new evidence becomes available. Although some taxonomists consider there to be up to 16 distinct families, most recognize 11 families: Alestiidae, Anostomidae, Characidae, Citharinidae, Ctenoluciidae, Curimatidae, Erythrinidae, Gasteropelecidae, Hemiodontidae, Hepsetidae, and Lebiasinidae. These families encompass species that are diverse in life form and behavior, with examples including the blind cavefish and predatory piranhas, as well as popular aquarium species such as tetras.

African pike (*Hepsetus odoe*) foam nest in the Okavango Delta in Botswana. (Photo by Animals Animals ©C-Par Farnetti, OSF. Reproduced by permission.)



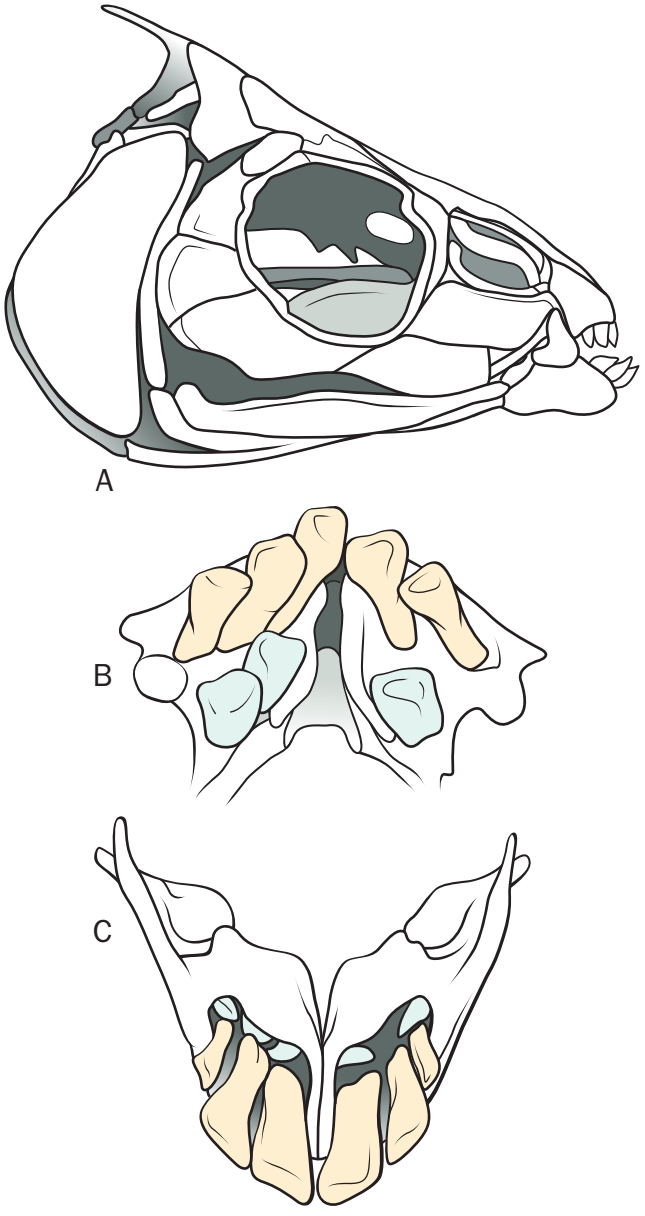
Piranha spawning behavior. (Illustration by Patricia Ferrer)

A silver tetra (*Poptella orbicularis*) living in the Peruvian Amazon. (Photo by David M. Schleser/Nature's Images, Inc./Photo Researchers, Inc. Reproduced by permission.)

Physical characteristics

Most species of Characiformes are small fishes, although size and shape vary widely throughout the order. The smallest member of the order is the Bolivian pygmy blue characin (*Xenurobrycon polyancistrus*), which attains a maximum size of around 0.5 in (1.4 cm); the largest species, the giant tigerfish (*Hydrocynus goliath*) grows to 4.3 ft (1.33 m).

Most Characiformes are brightly colored and often silvery, but some are also brilliant shades of red or blue. Characiformes vary widely in body form. Some species have long and slender bodies, while others, such as hatchetfishes, are deep-bodied and laterally compressed. The body is covered in scales, and the lateral line is often decurved or may be incomplete in some species. Most species have an adipose fin, a short fin between the dorsal and caudal fins. Pelvic fins generally have five to twelve rays, and the anal fin may be short to moderately long, with 45 rays or fewer. Characiformes lack sensory barbels, but they typically have large eyes to heighten visual acuity.



Skull showing replacement teeth (in blue)—an important feature of this group of fish. (Illustration by Patricia Ferrer)

Distribution

Characiformes are found in fresh waters of Texas and Mexico in North America and are widely distributed in Central America, South America, and Africa. Over 1,300 species, 252 genera, and 10 families inhabit South America. At least 176 species in 23 genera and 4 families occur throughout Africa.

Habitat

As a dominant group of freshwater fishes, Characiformes inhabit all types of fresh waters, including weedy river edges, stagnant ponds, rushing streams, and even underground caves. Certain species also possess morphological adaptations, including the ability to breath air or swollen lips that facilitate gas exchange in the upper portion of the water column, that enable them to move into shallow waters of floodplains and flooded forests.

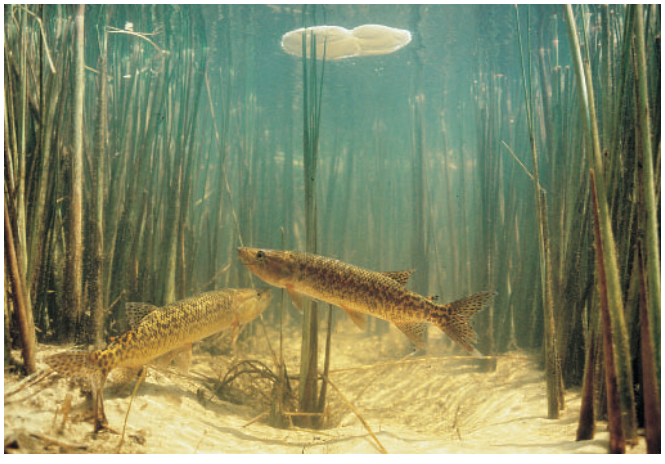
Behavior

The diversity of species represented by the Characiformes necessitates a diversity of behaviors. Many species travel in schools under certain conditions. Some species, such as members of the Ctenoluciidae, form schools as juveniles but become solitary as adults. Other species, including members of the Curimatidae, piranhas, and tetras, travel in large aggregations during all life stages. However, certain species, such as the blind cavefish, rarely gather in groups, and do not form organized aggregations. Although many of the smaller species of Characiformes live their whole lives in a limited geographic area, some species undertake extensive seasonal or spawning migrations.

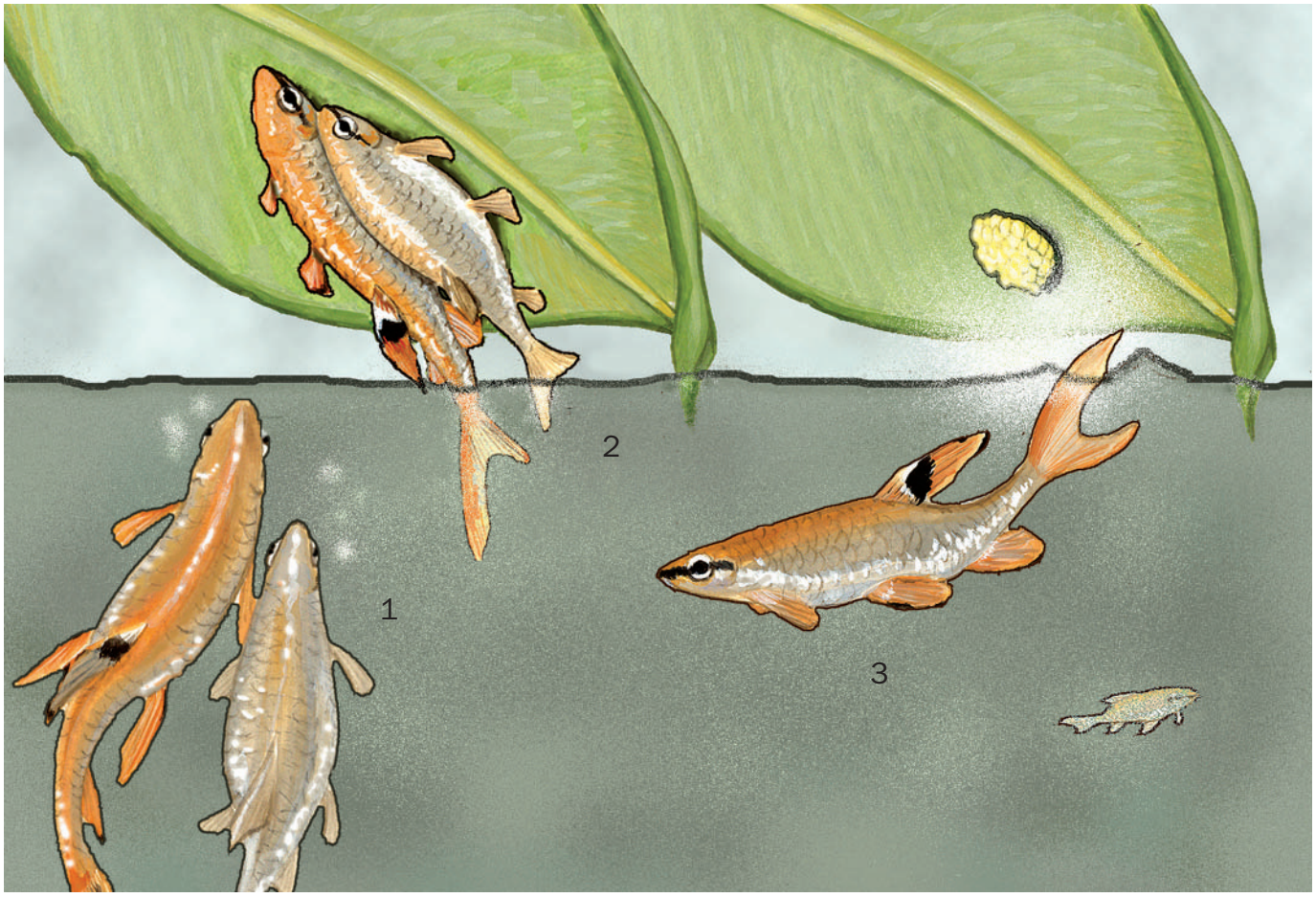
Courtship behaviors and migrations are associated with spawning in some members of the Characiformes. These unique courtship behaviors often involve fin displays to attract mates as well as elaborate swimming patterns to lure the mate to the spawning site. In addition to complex courtship rituals, some species possess morphological adaptations to attract mates. Males of certain species may utilize sensory cues, including pheromones and visual lures, to gain the attention of females.

Feeding ecology and diet

As reflected by their diversity of body shapes, Characiformes exhibit remarkable feeding specializations and exploit all available trophic modes. Many predatory species, particularly those of the Characidae, have well-developed teeth that enable them to feed on other fish. Some species, such as tigerfishes, solitarily stalk their prey: others, such as piranhas, engage in voracious group predation. Other carnivorous species



African pike (*Hepsetus odoe*) adults guard their foam nest in the Okavengo Delta in Botswana (Photo by Animals Animals ©Partridge OSF. Reproduced by permission.)



Tetra mating: 1. Tetra pair (*Copella arnoldi*) swim toward the surface, seeking suitable site to lay eggs (male left, female right); 2. The pair attaches briefly to the underside of a leaf, where the female lays eggs and the male fertilizes them. They repeat until all eggs are laid; 3. The female leaves, but the male cares for eggs until they hatch, using his long caudal fin to splash them and keep them moist. (Illustration by Gillian Harris)

pick or suck invertebrates from the substrate. In contrast, some Characiformes are strictly herbivorous, feeding on plants, fruits, or seeds. Other species filter plankton or are detritivores that feed on mud, algae, and ooze. Among the most remarkable feeding adaptations observed in freshwater fishes, certain Characiformes survive by eating the scales or pieces of fins from other fishes.

Many Characiformes are small-bodied and, thus, fall prey to larger fish species. In fact, predatory piranhas may indiscriminately attack a variety of food items, including smaller characins. Humans are the major predator of some characins. Small species are harvested as bait for fisheries and as trade items for the aquarium industry. A variety of the larger species, particularly tigerfishes, pacus, and piranhas, sustain important local fisheries in South America and Africa.

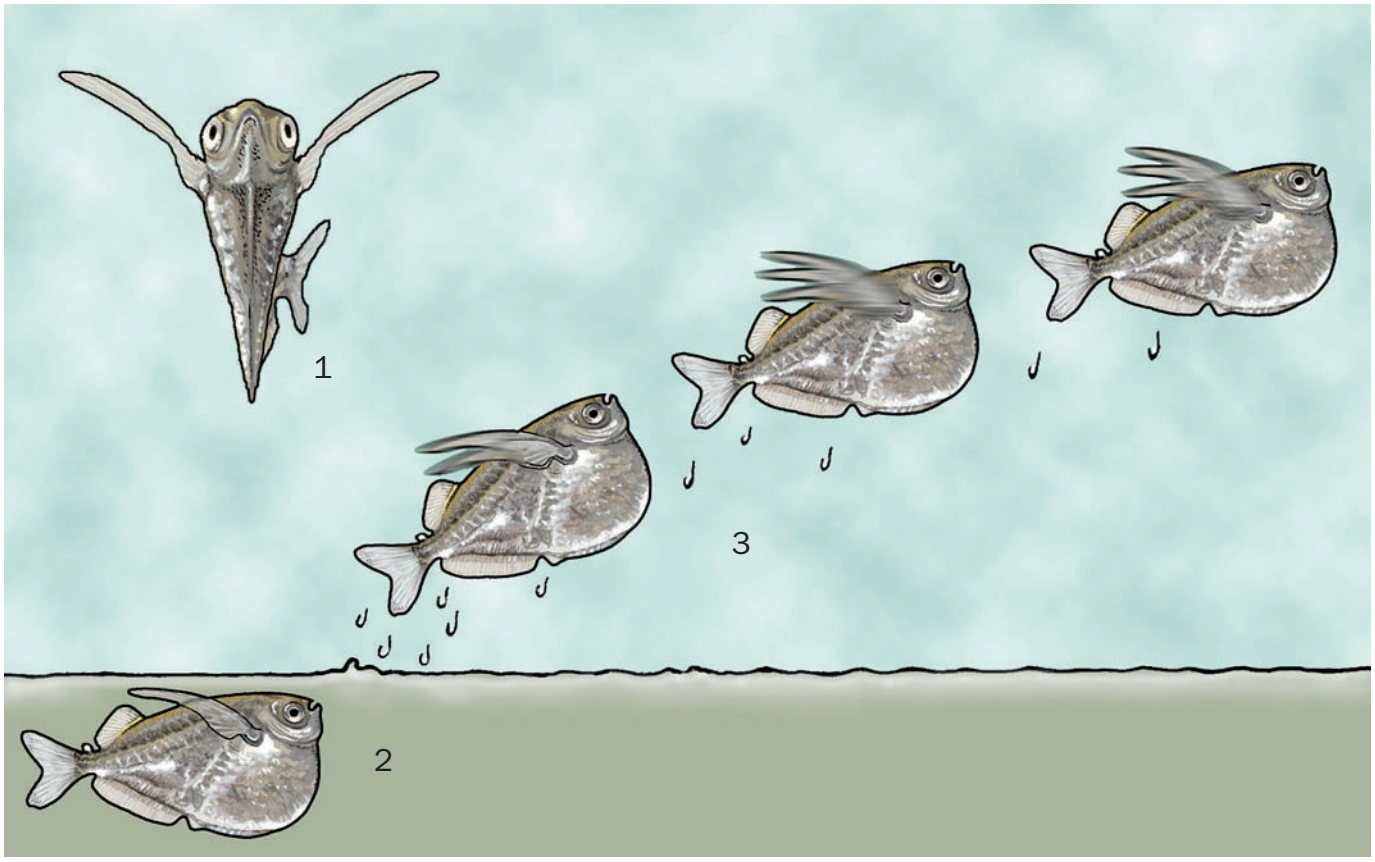
Reproductive biology

Most Characiformes broadcast their eggs and devote little parental care to their young. The eggs are often scattered among aquatic plants, and the vegetative cover confers some protection to young by providing shelter from predators. In a few species, including members of the Characidae, the male inseminates the female, and she may retain the sperm cells in her ovary for a period of days to months. However, fertilization does not take place until the eggs and sperm are shed into the water column at the same time.

Certain Characiformes exhibit an assortment of more specialized breeding behaviors. Members of the Erythrinidae construct nests for their eggs, and the African pike characins of the family Hepsetidae deposit eggs in a bubble-like nest of floating foam. To avoid egg predation, female splash tetras (*Copella arnoldi*) jump out of the water and lay their eggs on the underside of overhanging vegetation or rocks. The males follow, fertilize the eggs, and remain in the area to splash water onto the eggs until they hatch. Members of another species, *Brycon petrosus*, crawl onto the banks of rivers to lay their eggs.

Conservation status

The IUCN Red List includes 7 Characiformes. Six are listed as Data Deficient, and one, the naked characin (*Gymnocharacinus bergii*), is listed as Endangered. Although international conservation concerns have not been recognized for other



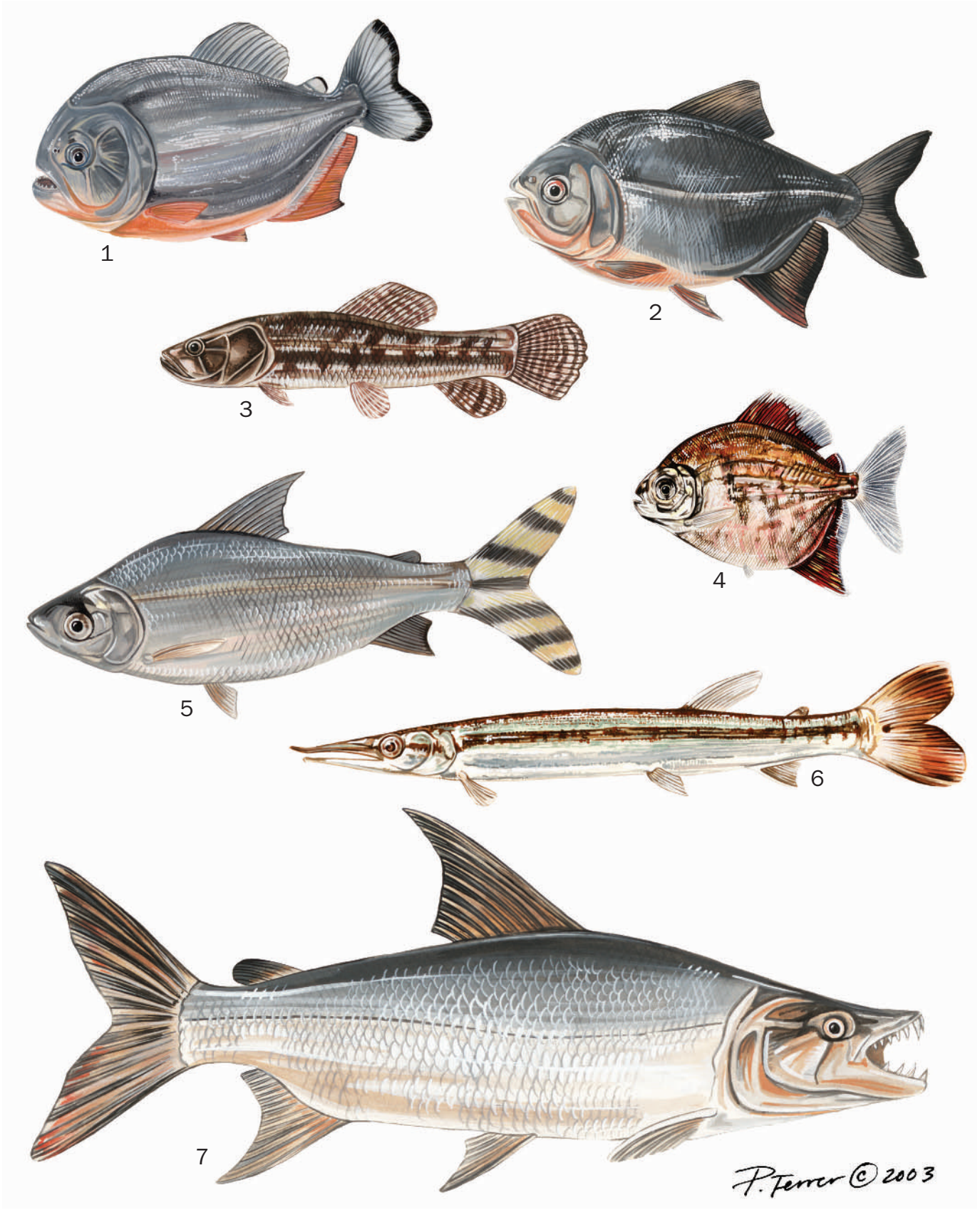
The "flying" hatchetfish: 1. River hatchetfish (*Gasteropelecus sternicla*), front view showing its thin body and long pectoral fins; 2. Hatchetfish swims just beneath the surface; 3. Launches itself out of the water, leaping into the air and staying aloft for some distance by rapidly beating its pectoral fins. (Illustration by Gillian Harris)

species, many Characiformes are harvested for the aquarium trade, an industry that is monitored and regulated only in certain countries or localities.

Significance to humans

Many Characiformes, including tetras, hatchetfishes, and pencilfishes, are popular aquarium fishes. Others are important as a food resource for humans. Although some species are traded commercially, many are relied upon to meet the subsistence food needs of communities living along tropical rivers. Examples include members of the Citharinidae (dorados) and Serrasalminae (tambaqui and pacus). In addition, some Characiformes, such as tigerfishes, are popular recreational targets that attract anglers from around the world.

1. Splash tetra (*Copella arnoldi*); 2. False rummynose tetra (*Petitella georgiae*); 3. Bleeding-heart tetra (*Hyphessobrycon erythrostigma*); 4. Cardinal tetra (*Paracheirodon axelrodi*); 5. Blind cavefish (*Astyanax mexicanus jordani*); 6. Striped African darter (*Nannocharax fasciatus*); 7. Striped headstander (*Anostomus anostomus*); 8. River hatchetfish (*Gasteropelecus sternicla*). (Illustration by Patricia Ferrer)



1. Red-bellied piranha (*Pygocentrus nattereri*); 2. Pirapitinga (*Piaractus brachypomus*); 3. Trahira (*Hoplias malabaricus*); 4. Silver dollar (*Myleus pacu*); 5. Flagtail prochilodus (*Semaprochilodus taeniurus*); 6. Golden pike characin (*Boulengerella lucius*); 7. Giant tigerfish (*Hydrocynus goliath*). (Illustration by Patricia Ferrer)

Species accounts

Giant tigerfish
Hydrocynus goliath

FAMILY
Alestiidae

TAXONOMY
Hydrocynus goliath Boulenger, 1898, Kinshasa and Umangi, Upper Congo.

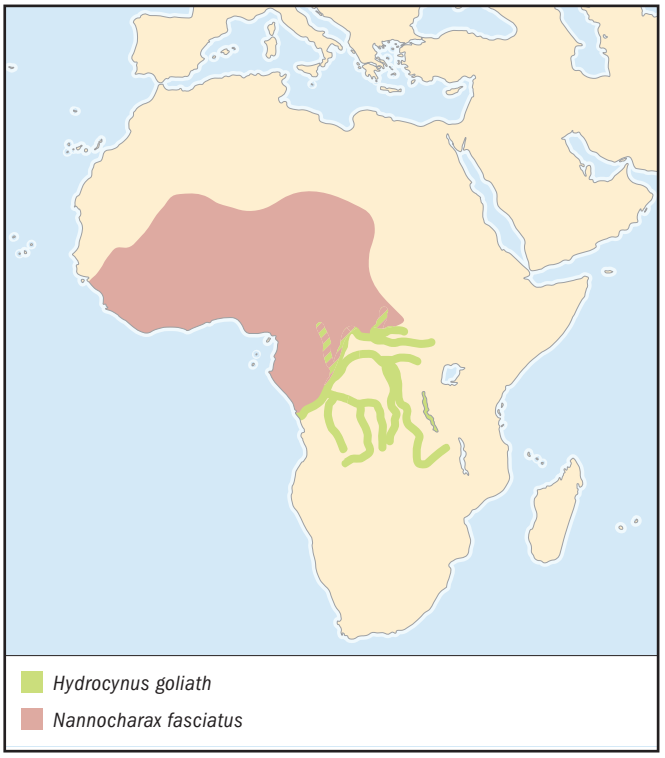
OTHER COMMON NAMES
German: Wolfsalmler.

PHYSICAL CHARACTERISTICS
The largest characin, reaching a maximum reported fork length of 4.3 ft (1.33 m) and weight of 110 lb (50 kg). The fish has an elongate, fully scaled body, with a high dorsal fin and deeply forked caudal fin. The body appears silvery, but the back is a darker gray. The fins are often orange or red, and the fish may become brightly colored during the breeding season. The sharp canine teeth are placed alternately on the upper and lower jaws.

DISTRIBUTION
Africa in the Congo River basin, Lualaba River, Lake Upemba, and Lake Tanganyika.

HABITAT
Large rivers and nearshore areas of lakes.

BEHAVIOR
Tigerfish aggregate with similar-sized individuals of the same species, sometimes in schools. Smaller fish occur in large aggregations; large fishes gather with few members in the group. This species migrates in rivers to find appropriate spawning sites.



FEEDXING ECOLOGY AND DIET
Adults are voracious predators that consume a wide variety of smaller fish. Larvae eat zooplankton, but they quickly move to larger prey as they grow. Juveniles and subadults are vulnerable to crocodiles, otters, and a great variety of predatory fishes and fish-eating birds. Humans are the only known predators of aduts.

REPRODUCTIVE BIOLOGY
Spawning takes place during the summer along the shores of lakes and flooded banks of large rivers. Females disperse hundreds of thousands of eggs into flooded vegetation, where they hatch and develop with no parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is known internationally as a sport fish and attracts anglers from around the world. It also is sought in local commercial and subsistence fisheries in several African countries, including Tanzania and Zambia. ◆

Striped headstander
Anostomus anostomus

FAMILY
Anostomidae

TAXONOMY
Anostomus anostomus Linnaeus, 1758, South America.

OTHER COMMON NAMES
English: Striped anostomus; German: Prachtkopfsteher; Spanish: Anostomus rayados, lisa; Portuguese: Anostomo.

PHYSICAL CHARACTERISTICS
Maximum total length 6.3 in (16 cm). Has elongated body with head that tapers to pointed nose, and small upward-facing mouth. Three dark longitudinal stripes start at front of body and extend to tail area; stripes widen as the fish ages. Area between the stripes is gold or mustard color. All fins have red bases; a red spot is apparent on the dorsal fin.

DISTRIBUTION
South America in inland streams and rivers of the Amazon, Orinoco, and Essequibo River basins.

HABITAT
Mainly weeds, rocks, and woody debris of tropical rivers.

BEHAVIOR
Often nips at fins of other fishes under aquarium conditions. Swim in slow-moving schools, generally with their heads down, although may tilt the head backward at times while feeding.

FEEDING ECOLOGY AND DIET
Feeds on worms, crustaceans, insects, and plant material.

REPRODUCTIVE BIOLOGY
Scatters eggs and fertilizes them in the water column. Few additional details are known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular aquarium fish. ◆

Blind cavefish
Astyanax mexicanus jordani

FAMILY
Characidae

TAXONOMY
Astyanax mexicanus jordani Hubbs and Innes, 1936, San Luis Potosí, Mexico.

OTHER COMMON NAMES
English: Blind cave characin, blind cave tetra; German: Blinder Höhlensalmler; Spanish: Sardina ciega; Portuguese: Peixe-caverna, Peixe-cego.

PHYSICAL CHARACTERISTICS
Maximum length 3.5 in (8.9 cm). The species evolved in the darkness of caves. Perhaps because of the absence of light in the environment, the body lacks pigments; instead, it is peach-colored with a silvery sheen. Has a complete lateral line along the body. Fins are colorless and transparent. Another characteristic attributed to the dark environment are vestigial eyes; the eye depressions are covered by skin and other tissue.

DISTRIBUTION
Mexico.

HABITAT
Subterranean lakes, streams, and pools of underground caves.

BEHAVIOR
Despite a lack of vision, this species exhibits exceptional navigation abilities. The lateral line is highly sensitive to vibrations, which allows the fish to find food and avoid obstacles as they swim. A solitary species, there is little interaction between individuals.

FEEDING ECOLOGY AND DIET
General, omnivorous feeders that primarily consume benthic invertebrates and algae. Use their excellent sense of smell to locate food items.

REPRODUCTIVE BIOLOGY
Spawns by broadcasting eggs. The male and female swim alongside each other near the surface of the water, with their ventral surfaces pressed together; the female scatters eggs, which are then fertilized by the male. The eggs fall to the bottom and hatch in two to three days. The larvae have normal eyes when they hatch, but these become enclosed in tissue after a few weeks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Commonly kept in aquaria, but not as popular as most other characins. Studies of this species have provided useful insights into the evolution of eyes and sight, which can also help improve scientific understanding of human vision. ◆

Bleeding-heart tetra
Hyphessobrycon erythrostigma

FAMILY
Characidae

TAXONOMY
Hyphessobrycon erythrostigma Fowler, 1943, Peru-Brazil border.

OTHER COMMON NAMES
English: Tetra perez; German: Fahnen-Kirschflecksalmler, Perez Salmler; Spanish: Mojarita, punto rojo.

PHYSICAL CHARACTERISTICS
Standard length 2.4 in (6.1 cm). Deep-bodied fishes that are orange to brown in color on the back and belly. The scales and fins are reddish pink, with a red spot behind the gill cover along the deeply colored lateral line. Dark spots are prominent on the dorsal fin, and the long rays of the dorsal fin are highly arched in males. The anal fin is elongate, stretching from mid-body to near the caudal fin. This fin is white in males, a feature that distinguishes them from females, in which the fin is transparent gray.

DISTRIBUTION
Upper Amazon basin of South America.

HABITAT
Occur in the bottom portion of the water column in freshwater tropical habitats, preferring temperatures of approximately 73–82°F (23–28°C). Individuals often live in vegetation and woody debris.

BEHAVIOR
Schooling fishes; little is known of their activities, social behavior, or reproductive behavior in nature.

FEEDING ECOLOGY AND DIET
Omnivore; primarily consumes insects and crustaceans. Because of its small size, succumbs to predation by a variety of larger fishes.

REPRODUCTIVE BIOLOGY
Females deposit 20–30 eggs in vegetation during each mating act. The eggs incubate for approximately 48 hours in aquaria; fry emerge in three days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular aquarium fish that are valued for their bright colors. ◆

Silver dollar
Myleus pacu

FAMILY
Characidae

TAXONOMY
Myleus pacu Jardine and Schomburgk, 1841, Guyana.

OTHER COMMON NAMES
English: Pacu, pacupeba; German: Brauner Mühlsteinsalmler; Portuguese: Pacu dente; Creole: Koumarou-nwé, pakou.

PHYSICAL CHARACTERISTICS
Maximum length 8 in (20 cm). This species is deep-bodied with a small head and a broad mottled reddish brown body. A row of scutes occurs along the edge of the belly, and the body scales are small. Two rows of teeth are found on the upper jaw; the front row is incisor-like, the back row contains molars.

DISTRIBUTION
South America in Guyana, French Guiana, Brazil, Suriname, and Bolivia.

HABITAT
Inhabits streams and main stems of rivers.

BEHAVIOR
Gregarious and rarely aggressive. During the rainy season, large groups migrate to small creeks to reproduce.

FEEDING ECOLOGY AND DIET
Although their powerful dentition can cause serious bites, silver dollars are herbivores that feed primarily on aquatic plants (often of the family Podostemaceae). Occasionally, they also consume seeds and fruits, which they crush with their large molars. Predators include larger carnivorous fishes, caimans, otters, river dolphins, and a wide variety of fish-eating birds. Some fish are also taken by humans.

REPRODUCTIVE BIOLOGY
Reproduce by external fertilization. Females and males swim through the water together; females broadcast eggs into the water column, where they are fertilized by males. No parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Common aquarium fishes throughout the world. Also provide an important food source for many communities living near streams inhabited by pacus. ◆

Cardinal tetra
Paracheirodon axelrodi

FAMILY
Characidae

TAXONOMY
Paracheirodon axelrodi Schultz, 1956, Rio Negro, Brazil.

OTHER COMMON NAMES
English: Red neon, neon tetra, scarlet characin; German: Kardinaltetra, Roter Neon.

PHYSICAL CHARACTERISTICS
Maximum standard length 1 in (2.5 cm). One of the most colorful of the characoids. Although the dorsal portion is gray,

the sides are marked with an iridescent turquoise-blue stripe and the lower flanks are bright red. The dorsal fins exhibit a peculiar blue-green iridescence.

DISTRIBUTION
Upper Rio Orinoco and upper Rio Negro of South America.

HABITAT
This species inhabits a wide variety of habitats. It is often found in shaded or vegetated areas of small, slow-moving, clear, and blackwater creeks. During the rainy season, the fish move into headwaters and flooded forests of rivers. At times of low water, it lives along the margins of lakes or becomes concentrated in creeks and backwaters.

BEHAVIOR
Often aggregates in shoals of 12–30 individuals in middle portions of the water column. Individuals move onto the floodplain during the rainy season. They are considered "annual fishes," spawning during the spring floods and often perishing due to starvation when foraging habitats retract during the subsequent low-water season.

FEEDING ECOLOGY AND DIET
Feeds mainly on worms and small crustaceans. Due to its small size, indiscriminately consumed by many larger piscivores, including piranhas.

REPRODUCTIVE BIOLOGY
Spawns on floodplains of rivers as water levels rise during the rainy season. Females bear 300–500 large eggs; these are broadcast into the water column and fertilized by males. In captivity, eggs hatch in 24–30 hours; fry become free-swimming after three to four days.

CONSERVATION STATUS
Not listed by the IUCN. However, this species accounts for 80% of the total catch of ornamental species in some areas, such as the state of Amazonas in Brazil, and this high level of extraction to support the aquarium trade has resulted in local regulations that restrict harvests during the spawning season.

SIGNIFICANCE TO HUMANS
One of the most popular aquarium fishes throughout the world, its commercial harvest for the aquarium trade also supports the economic and social structure of many human communities along the rivers it inhabits in South America. ◆

False rummynose tetra
Petitella georgiae

FAMILY
Characidae

TAXONOMY
Petitella georgiae Gery and Boutiere, 1964, Rio Huallago, Peru.

OTHER COMMON NAMES
English: False rednose tetra, false rummy-nosed tetra; German: Rotmaulsalmler; Finnish: Punapää tetra; Polish: Czerwonoglówka.

PHYSICAL CHARACTERISTICS
Maximum size 1.5 in (3.9 cm). These fish appear iridescent and shiny in water. The body is silver to olive-brown, with a gold stripe extending from the head to the base of the tail. The head and the iris of the eye are bright red. The tail is deeply forked and striped, with three black and four white bands. All fins other than the caudal fin are transparent.

DISTRIBUTION
South America in the upper Rio Amazonas basin in Peru, as well as in the Purus, Negro, and Madeira basins in Brazil.

HABITAT
Swift-moving headwater streams, often preferring the cover of vegetation if available.

BEHAVIOR
A schooling species; other behavioral features have not been described.

FEEDING ECOLOGY AND DIET
Feeds on benthic algae, plants, and crustaceans in the plankton and benthos. Its small size makes it susceptible to predation by many larger species of fish as well as water snakes and many different fish-eating birds.

REPRODUCTIVE BIOLOGY
Reproduces by scattering eggs; females broadcast eggs into the water column, and these eggs are fertilized by the males. Mating activity typically occurs near vegetation in the evening.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An important aquarium species. ◆

Pirapitinga

Piaractus brachypomus

FAMILY
Characidae

TAXONOMY
Piaractus brachypomus Cuvier, 1818, Brazil.

OTHER COMMON NAMES
English: Cachama, freshwater pompano, pacu, red pacu, red-bellied pacu; German: Gamitana-Scheibensalmler, Riesenpacu; Spanish: Cachama, cachama blanca, morocoto, paco; Portuguese: Caranha, pirapitinga.

PHYSICAL CHARACTERISTICS
Total length 34.6 in (88 cm). Deep-bodied; appears silvery gray on back and sides, but areas under the throat, along the belly, and at the edges of the pelvic and anal fins are red. Unlike in other Characiformes, the adipose fin contains rays in adults.

DISTRIBUTION
Amazon and Orinoco River basins in South America. Feral individuals have been caught in 16 states throughout the United States, likely as a result of releases from personal aquariums or fish farms.

HABITAT
Pelagic; occurs in streams and tributaries to main river channels, also in ponds and oxbow lakes.

BEHAVIOR
Young live in flooded savanna vegetation until about two years old, then move into flooded forests with adults. Feeds during rainy seasons. During low water and just before the start of the second rainy season of the year, adults move upstream in schools to spawn.

FEEDING ECOLOGY AND DIET
Primarily herbivorous, although it possesses powerful teeth that could inflict severe bites. Feeds mostly on plants and detritus, but may also consume nuts, fruits, seeds, and sometimes insects. Juveniles are vulnerable to larger predatory fishes, notably giant pimelodid catfishes, caimans, otters, and a variety of fish-eating birds. Adults have few predators because of their large size but can be preyed upon by jaguars.

REPRODUCTIVE BIOLOGY
Spawns as waters begin to rise during the second rainy season. Do not feed during spawning but live off fat stored during the wet season. Eggs are scattered and fertilized in the water column. Males and females mature around seven years of age.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
One of the most important commercial species in the Amazon basin. Popular food fishes, they are taken in wild fisheries in their native range and raised in fish farms in North and South America. Also popular in aquaria. ◆

Red-bellied piranha

Pygocentrus nattereri

FAMILY
Characidae

TAXONOMY
Pygocentrus nattereri Kner, 1858, Brazil.

OTHER COMMON NAMES
English: Red piranha, redbelly piranha; German: Diamantpiranha, Schulterfleck-Piranha; Natterers Sägesalmler; Spanish: Caribe boca de locha, palometa, paña; Portuguese: Piranha caju; piranha-quexicuda.

PHYSICAL CHARACTERISTICS
Average length of adult 6–8 in (15.2–20.3 cm), but can grow up to 12 in (30.5 cm). Male and female red piranhas are alike externally, with body height about one-half body length. The stocky bodies have reddish bellies, though overall coloration varies depending on location and age. Sides often pale brown to slightly olive; back bluish gray to brownish; throat belly areas bright red. Forked caudal fin usually gray. Pectoral, pelvic, and anal fins typically bright red. Powerful jaws with triangular, interlocking sharp teeth.

DISTRIBUTION
Widely distributed in South America and in basins of the Amazon, Paraguay-Paraña, and Essequibo Rivers, as well as coastal rivers of northeast Brazil.

HABITAT
Creeks and interconnected ponds; prefers areas with dense vegetation.

BEHAVIOR
Diel activity varies by age; adults forage mainly at dusk and dawn, medium-sized individuals are most active at dawn, late afternoon, and night. Smaller fishes feed during the day. Exhibits a "lurking, then dashing" sequence of behaviors during the day. Hierarchical structure often exists in small schools.

FEEDING ECOLOGY AND DIET
Feeds communally, with groups of 20–30 individuals waiting in vegetation to ambush prey. Prey are attacked in a feeding frenzy, further induced by the presence of blood in the water. Highly predaceous carnivores, but also scavenge for food and consume insects, snails, worms, plants, and fins of other fishes. Can feed continuously and maintain a voracious bite by replacing teeth on alternate sides of the jaw. Preyed upon by other fishes (including large pimelodid catfishes), crocodilians, fish-eating birds, and large mammals (including jaguars).

REPRODUCTIVE BIOLOGY
Spawns through external fertilization. After elaborate courtship display involving swimming in circles, the female deposits layers of eggs on plants in the water, and the male fertilizes them. The male guards and fans the egg masses until they hatch in 9 to 10 days. Annual reproductive success varies, but is dependent upon the degree to which the savanna is flooded.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is kept as an aquarium fish. This activity is illegal in some states of the United States to prevent irresponsible hobbyists from releasing the species into the wild, where it may multiply and prey upon indigenous fish species. These fish can also inflict serious bites, although they are not as aggressive as once believed, and they are unlikely to attack humans unless the human is bleeding or in water near congregations of other prey species. The species is commonly caught and eaten by river dwellers throughout its extensive range. Large numbers are also caught for use as trot-line bait for large catfishes. ◆

Striped African darter
Nannocharax fasciatus

FAMILY
Citharinidae

TAXONOMY
Nannocharax fasciatus Guenther, 1867, Gabon.

OTHER COMMON NAMES
English: African darter tetra; German: Afrikanischer Bodensalmler.

PHYSICAL CHARACTERISTICS
Maximum length 2.6 in (6.6 cm). These fish have a short, blunted snout and a thin, elongate body. The body is golden brown on the back, with a dark lateral line midbody, below which is light brown to white. The pigmentation is marked by seven to eleven dark brown transverse bands across the back along the length of the body. The fins are also marked with spots forming transverse bands; a large dark spot is on the anal and adipose fins. The tip of the dorsal fin is red in adults. An elongate pectoral fin extends to the origin of the pelvic fins.

DISTRIBUTION
Throughout equatorial West Africa.

HABITAT
Clear, swift-moving waters in forested regions; often found over sandy substrates or in similar open areas.

BEHAVIOR
These fishes live near the water bottom, often in contact with the substrate. They swim with their heads up at an angle of 45° and use long pectoral fins for support while searching for food along the bottom. They rest for longer periods on their pectoral, pelvic, and caudal fins.

FEEDING ECOLOGY AND DIET
Consumes small invertebrates, including insect larvae, worms, ostracods, and zooplankton near the substrate. Because of their small size, likely consumed by a variety of larger predators.

REPRODUCTIVE BIOLOGY
Reproduces externally; females scatter eggs in the water column, where they are fertilized by males. Eggs are released in partial batches during several spawning events. There is no parental care.

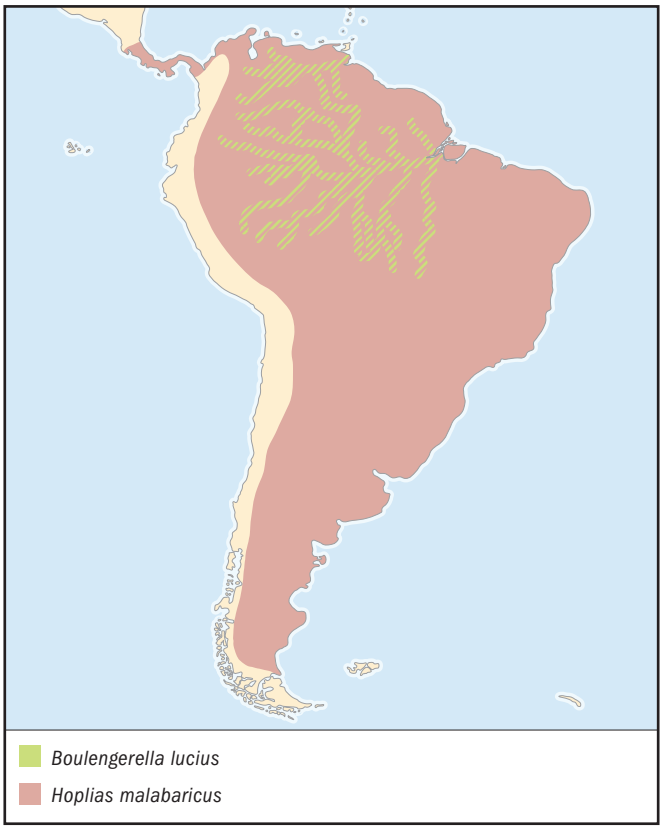
CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes kept as aquarium fishes and traded commercially as part of the ornamental fish industry. ◆

Golden pike characin
Boulengerella lucius

FAMILY
Ctenoluciidae

TAXONOMY
Boulengerella lucius Cuvier, 1816, Brazil.



OTHER COMMON NAMES
English: Cuvier's pike characin; German: Cuviers Hechtsalmler; Portuguese: Pirapacu.

PHYSICAL CHARACTERISTICS
Standard length 16.5 in (42 cm). Elongated, slender fishes resembling North American pikes. Dorsal fin is located toward the back of the body; the anal fin is short. Fishes are metallic green on the back, lighter on sides, and silvery on belly. A small dark spot on caudal fin helps distinguish this species from others in the genus. The jaw terminates in a long fleshy filament and contains numerous teeth.

DISTRIBUTION
Inland waters of the Amazon, Rio Negro, and Rio Orinoco River basins in South America.

HABITAT
Pelagic; inhabits open waters of large rivers.

BEHAVIOR
Migrates upriver to spawn during the rainy season.

FEEDING ECOLOGY AND DIET
Predatory; eats many species of smaller fishes available in open water areas. Predators have not been specified.

REPRODUCTIVE BIOLOGY
Breeds by external fertilization of eggs. Females release eggs into the water column, where they are fertilized by males. Eggs are demersal, meaning they sink to the bottom.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Exploited by humans as a subsistence and commercial food fish; also exported as part of the aquarium trade. ◆

Flagtail prochilodus
Semaprochilodus taeniurus

FAMILY
Curimatidae

TAXONOMY
Semaprochilodus taeniurus Valenciennes, 1817, Amazon River.

OTHER COMMON NAMES
English: Silver prochilodus; German: Nachtsalmler, Schwanzstreifensalmler; Finnish: Juovahuulitetra; Portuguese: Jaraqui, jaraqui escama fina.

PHYSICAL CHARACTERISTICS
Standard length 9.4 in (24 cm). Like other members of this family, has many small teeth on the jaws and a mouth with enlarged fleshy lips that can be turned outward to form a rasping or suction disk. The lips are often lined with fine papillae, thus the name "flannel mouths." Deep-bodied; dark gray on the back fading to silvery hues on the flanks. Dorsal, anal, and adipose fins are dark gray; pectoral and pelvic fins are nearly clear. Edges of the dorsal and anal fins appear yellow. The caudal fin is most striking, yellow with prominent black horizontal stripes.

DISTRIBUTION
Central portion of the Amazon River basin in Brazil.

HABITAT
Main channels of streams and rivers, as well as floodplain lakes.

BEHAVIOR
Undertakes annual migrations for spawning, feeding, and dispersal. At the beginning of the flood season, schools of mature fish migrate downstream from tributaries to the Amazon River to spawn. Migration occurs during the day; spawning takes place at night. After spawning, small groups move into flooded forests of their home tributaries to feed. As soon as the water levels begin to fall, adults undertake a complex dispersal migration. They move back into the main channel of the Amazon and migrate upstream, before dispersing into tributaries other than those in which they lived the year before.

FEEDING ECOLOGY AND DIET
Primarily consumes plants, algae, and other detritus. It can use its lips as suction cups to eat detritus attached to trees and other submerged vegetation in the flooded forest. Large quantities of mud are often reported in the stomach. Although the fishes are moderate in size, they are preyed upon by larger predatory fishes, such as catfishes.

REPRODUCTIVE BIOLOGY
Spawning may occur in shallow water along the course of large rivers, sometimes below barriers such as waterfalls. Males emit loud, grunting noises to attract females to the spawning areas. Females scatter a single batch of small eggs into well-oxygenated waters. The eggs and fry are carried passively downstream and eventually onto the floodplain, where they begin feeding. After two years, these offspring spawn for the first time.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular worldwide as an aquarium species. As one of the most common species in the Amazon basin, it is an important food fish for local villages and towns. It is also traded commercially to areas outside the Amazon basin. ◆

Trahira
Hoplias malabaricus

FAMILY
Erythrinidae

TAXONOMY
Hoplias malabaricus Bloch, 1794, South America.

OTHER COMMON NAMES
English: Haimara, tararira, tararura, wolffish, wolf characin; French: Patagaye; German: Kleiner Trahira, Tigersalmler; Spanish: Perro de aqua, tararira; Portuguese: Dorme-dorme, lobó, traira, trairitinga; Palikur: Iigl.

PHYSICAL CHARACTERISTICS
Standard length 19 in (48.5 cm). Elongated, cylindrical body with short anal fin and large scales. Adipose fin is absent. Bodies of young have reddish brown back and yellowish belly, red bands across the head, and green band along the sides. Adults are mottled dull green and brown.

DISTRIBUTION
Inland waters of most river basins from Costa Rica to Argentina.

HABITAT
Lives in diverse habitats, ranging from clear streams to slow, turbid waters. Tolerates stagnant conditions in irrigation ditches, drainage channels, and floodplain ponds. Utilizes atmospheric oxygen, enabling it to inhabit low-oxygen habitats, including small brooks or ponds.

BEHAVIOR
Sedentary species, often remains in a relatively confined geographic area for life. It rests during the day and becomes active at night. These fish may form schools, typically in low numbers. They are ambush predators, waiting quietly under cover until suitable prey items approach.

FEEDING ECOLOGY AND DIET
Adults are voracious predators that feed on a wide variety of fish and shrimp. Juveniles eat crustacean and insect larvae, shrimp, and other small invertebrates. Trahiras are preyed upon by larger fishes, including piranhas and catfishes, as well as crocodilians, fish-eating birds, and otters.

REPRODUCTIVE BIOLOGY
Spawns over a protracted reproductive period, with multiple spawnings and size classes distributed uniformly throughout the year. Eggs are adhesive and placed in nests made in nearshore vegetation of shallow, slow watercourses. Male provides a high level of parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Supports important commercial fisheries in many countries of South America. Although displayed in some aquaria, not very popular as an aquarium species. ◆

River hatchetfish
Gasteropelecus sternicla

FAMILY
Gasteropelecidae

TAXONOMY
Gasteropelecus sternicla Linnaeus, 1758, Suriname.

OTHER COMMON NAMES
English: Common hatchetfish, silver hatchetfish; French: Poisson hachette argenté; German: Silberbeilbauchfisch; Spanish: Pechito, pechito plateado de raya negra; Portuguese: Borboleta, sapopema, voador.

PHYSICAL CHARACTERISTICS
Standard length 1.5 in (3.8 cm), but adults in aquaria may reach 2.4 in (6.5 cm). Females are larger than males. Deep, highly compressed body; belly profile creates a semicircular arc containing sternum and strong chest muscles. Pectoral fins are long and located high on the body near the head. Yellow to silver in color, with dark stripe running along the length of the body; fins are transparent.

DISTRIBUTION
South America in the upper Amazon basin, the Guyanas, and Venezuela.

HABITAT
Pelagic; lives near surface of slow waters in creeks and swamps. Often inhabits vegetated areas.

BEHAVIOR
Typically gregarious; lives in groups near surface of water. May be aggressive or calm. To avoid predators and capture insect prey, swims very fast to raise its body out of the water, then flies above the surface using its long pectoral fins. Unlike other "flying fish" that rely on gliding, it rapidly beats its pectoral fins to remain airborne for distances up to 10 feet (3 m).

FEEDING ECOLOGY AND DIET
Feeds on worms, crustaceans, and insects from the surface of the water, but also captures aerial insects. Predators are not specified in current literature, although likely eaten by a variety of larger fishes.

REPRODUCTIVE BIOLOGY
Spawns after a lengthy courtship. The female scatters eggs in the water or onto floating plants, where they are fertilized by males. The eggs then fall to the bottom or onto vegetation.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Common aquarium species. ◆

Splash tetra
Copella arnoldi

FAMILY
Lebiasinidae

TAXONOMY
Copella arnoldi Regan, 1912, Amazon River.

OTHER COMMON NAMES
English: Copeina, jumping characin, splashing tetra, spotted characin, spraying characin; French/Creole: Ti-yaya; German: Spritzsalmler; Finnish: Roiskuttajatetra; Polish: Smuklen pryskacz; Portuguese: Piratanta.

PHYSICAL CHARACTERISTICS
Small species, reaches a length of only 3 in (8 cm). The slender body is yellowish brown on the back, lighter on the sides, and almost white on the belly. The reddish, long, fanlike fins are particularly pronounced on males. There is a yellow spot at the base of the dorsal fin. Large scales with dark edges cover the body.

DISTRIBUTION
South America in the lower Amazon River basin and coastal portions of the Guyanas.

HABITAT
Swampy, slow-moving waters that often contain little oxygen.

BEHAVIOR
Remains near the surface of the water, likely a behavioral adaptation to life in stagnant, low-oxygen waters.

FEEDING ECOLOGY AND DIET
Feeds on a wide variety of insects and plant matter. Because of its small size and surface-living habits, it is likely preyed on by numerous larger fishes and fish-eating birds.

REPRODUCTIVE BIOLOGY
Male and female leap out of the water simultaneously and deposit a few eggs in a gelatinous mass on the underside of overhanging vegetation. They repeat this process until 60 or more eggs have been deposited. The male then uses its tail to splash water onto the eggs every 20–30 minutes until they hatch in two to three days. After hatching, the fry fall into the water.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular as an aquarium fish throughout the world. ◆

Resources

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Katherine E. Mills, MS
Elizabeth Mills, MS

Siluriformes
(Catfishes)

Class Actinopterygii
Order Siluriformes
Number of families 34

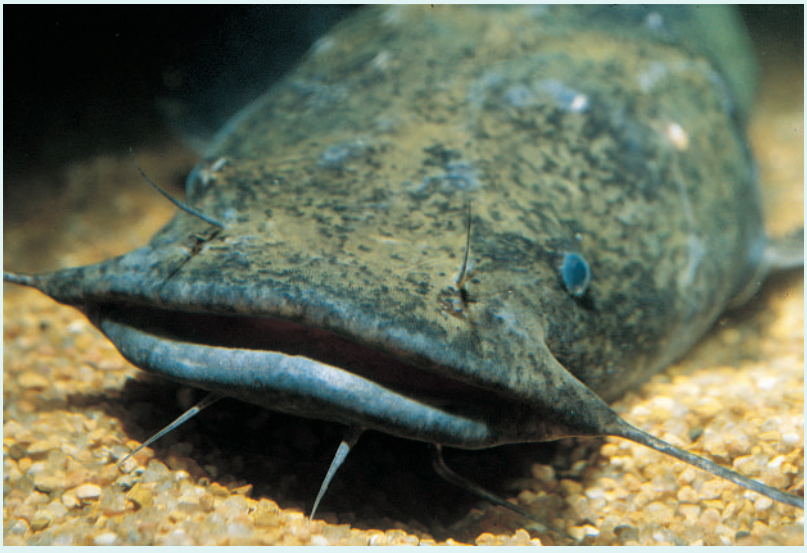


Photo: Flathead catfish (*Pylodictis olivaris*) genus fossils have been found dating back 15 million years. (Photo by Gary Retherford/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The late nineteenth century work of Carl H. Eigenmann and Rosa Smith Eigenmann on South American catfishes established the foundation upon which later researchers, such as William A. Gosline, George S. Myers, and Mario C. C. de Pinna, have built to clarify the classification of catfishes. However, the classification is still uncertain, and there is no full agreement among the authors about the relationships of the families. Most knowledge about the phylogeny of siluriforms comes from the research on Neotropical groups carried out in the last three decades of the twentieth century.

During the International Symposium on Phylogeny and Classification of Neotropical Fishes (Porto Alegre, Brazil, July 1997), de Pinna presented a talk about the interrelationships of Neotropical catfishes. He proposed a preliminary cladistic hypothesis that accepted 12 monophyletic groups of siluriforms. In at least three cases, the relationships between New World and Old World clades are well established: the South American diplomystids, the sister group to all other catfishes; the African mochokids, the sister group to the South American doradoid superfamily, which includes the doradids and the auchenipterids; and the South American aspredinids, the sister group to the Asian erethistids. Nevertheless, de Pinna's cladogram implies the existence of four more transcontinental phylogenetic relationships. The discovery of close interrelationships between systematic groups otherwise isolated in a continental block is relevant, due to the fact that most groups of ostariophysean fishes, such as siluriforms, primarily inhabit freshwaters.

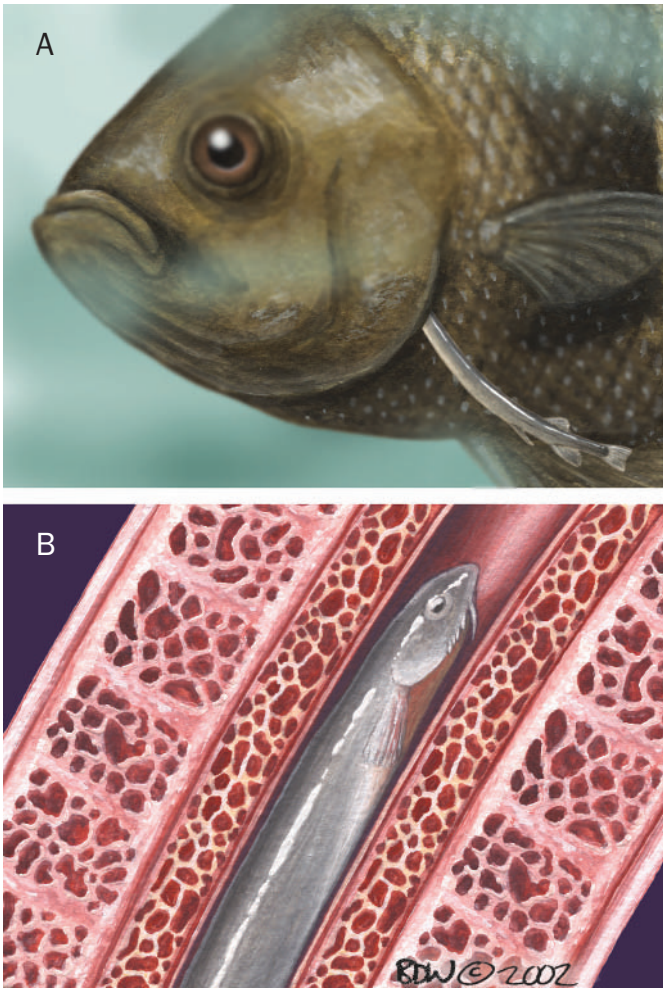
Catfish fossils include *Andinichthys*, *Incaichthys*, and *Hoffstetterichthys* (family Andinichthyidae) from the Upper Cretaceous and early late Paleocene of Bolivia; *Corydoras revelatus* (family Callichthyidae) from the late Paleocene of Argentina; *Hypsidoris farsonensis*, the only known species of the family Hypsidoridae, from the early middle Eocene of Wyoming, United States; late Eocene or early Oligocene (about 37 million years ago) material from Antarctica; *Hoplosternum* sp. (family Callichthyidae) from the middle Miocene of Colombia; and some material of the arioid (from the Arioida group) material from coastal marine Eocene deposits from Camden (Arkansas, United States).

It has been shown, based on cladistic grounds, that the gymnotiforms, or electric knifefishes, are the group most closely related to the siluriforms. Some authors have chosen to include both orders under the Siluriformes, a lead not followed here.

Physical characteristics

Catfishes are well known and recognized worldwide by a few characteristics. They normally show one to four pairs of barbels on the head around the mouth: one nasal, one maxillary, and two on the lower jaw or mandible. The nasal and/or lower jaw barbels may be absent, but in any case, the maxillary barbels are the longest. As these threadlike structures have plenty of taste buds, they have chemosensory and tactile functions, allowing the small-eyed catfishes to gather food efficiently.

Catfishes usually have spiny rays at the front of the dorsal and pectoral fins. These thornlike structures are large, unsegmented, and strong elements, technically similar to the other lepidotrichia, the rays that support the fins. Most families of siluriforms have two dorsal fin spines; the first is tiny, but very important, because it locks the second, larger spine in an erect position. A catfish with erected, pointed spines is nicely protected from most potential predators. The spines in some families also deliver a toxin produced in an associated venom



The parasitic catfish of the Amazon and Oranoco Rivers, known as the candiru (*Vandellia cirrhosa* and related species) usually feeds on blood from other fishes' gills (A). It detects the outward flow of nitrogen-rich water from the gills, but may confuse that with the outward flow of urine from a person urinating underwater. In this case, it has been known to swim into the urethra (B), where it feeds on blood, causing excrutiating pain. But the tight space and backward-pointing spines on the sides of its head make it impossible for the fish to turn around or back out, and it eventually dies inside the person. If not removed, it causes restriction or complete blockage of urination, massive infection, and often death. Native South Americans who live in its range typically wear protective garments when bathing or swimming in rivers. (Illustration by Bruce Worden)

gland. Although formidable weapons, spines are lacking in some catfish groups.

Most catfish species have a "naked" body because their leatherlike skin is completely scaleless. However, the so-called armored catfishes are covered at least partially by deeply embedded bony plates or by tubercles. Other external characteristics of catfishes are an adipose fin, usually present, sometimes rayed or preceded by a spine, and a small and toothless maxilla.

There are several internal characteristics worth mentioning, such as reductions, fusions, or absences in the set of skull bones typical of lower teleosts, as well as of intermuscular bones. The Weberian apparatus of catfishes involves five vertebrae, and their caudal skeleton is variable, ranging from six independent plates to the complete fusion of all its elements.

Distribution

Catfishes are mainly inhabitants of freshwaters, reaching their highest diversity in South America. There are more than 1,650 catfish species in South America distributed in eight monophyletic and endemic groups, including the richest family, the suckermouth armored catfishes (Loricariidae), with around 800 species. Loricariids and five other families form the armored catfishes, the largest monophyletic group of the order, with at least 1,150 species and a range between Costa Rica and Argentina. Included in this clade is the most speciose catfish genus, the plated catfishes *Corydoras* (Callichthyidae) with about 142 species. Other families of armored catfishes are the monotypic Nematogenyidae, the pencil or parasitic catfishes (Trichomycteridae), the spiny dwarf catfishes (Scoloplacidae), and the climbing, or South American hillstream, catfishes (Astroblepidae). The long-whiskered or antenna catfishes (Pimelodidae) used to be the second largest family, with about 300 species. However, since it is not a natural group, it was officially split in 2001 into three monophyletic families: the pimelodids (in the narrow sense), the heptapterids (Heptapteridae), and the pseudopimelodids (Pseudopimelodidae). In any case, Heptapteridae, the most species-rich group of the "old" long-whiskered catfishes with about 150 species, is widely distributed from Southern Mexico to Argentina. The remaining monophyletic groups of South American catfishes are the velvet or Patagonian catfishes (Diplomystidae), the whalelike catfishes (Cetopsidae), the doradoids (including the thorny or talking catfishes, Doradidae, and the driftwood catfishes, Auchenipteridae), and the banjo catfishes (Aspredinidae). The bullhead or North American freshwater catfishes (Ictaluridae), with 44 species, is officially the only family of the order endemic to North America, ranging as far south as Guatemala. The so-called Chiapas catfish was presented to the scientific community at the 2000 meeting of the American Society of Ichthyologists and Herpetologists; this unusual catfish seems to deserve its own family. So far, it is only known from southern Mexico.

Old World catfishes are also highly diverse; more than 1,000 species are known from Africa and Eurasia. The bagrid catfishes (Bagridae), the airbreathing or labyrinth catfishes (Clariidae), the glass catfishes (Schilbeidae), and the eeltail or tandan catfishes (Plotosidae) are the four families occurring in both Africa and Asia. Bagridae is the richest family of these widely distributed catfish clades, with about 130 species. The other three families include about 170 species. There are six catfish families endemic to Africa. Of them, the squeakers or upside-down catfishes (Mochokidae) is the richest, since it contains about180 species; two-thirds of which are included in the genus *Synodontis*. The loach or African hillstream catfishes (Amphiliidae) has about 60 species. Other endemic African families are the claroteids (Claroteidae), the auchenoglanidids (Auchenoglanididae), the electric catfishes (Malapteruridae), and the austroglanidids (Austroglanididae); together these four groups contain more than 100 species.

Asia is next to South America in the number of endemic catfish families. However, these tend to be poorly speciated groups, usually with fewer than 30 species each. The sucker or Asian hillstream catfishes (Sisoridae) is the richest family, with a few more than 110 species. Other endemic Asian families are the stream or shortfin catfishes (Akysidae) with 27 species, the shark catfishes (Pangasiidae) with 26 species, the torrent or Asian loach catfishes (Amblycipitidae) with 25 species, the erethistids (Erethistidae) with 13 species, and the armorhead or Chinese catfishes (Claroglanididae) and the squarehead or frogmouth catfishes (Chacidae), both with 3 species. The sheatfishes (Siluridae) is the only family of catfishes extending its range to Europe; it includes about 100 species, only 2 of which occur in Europe.

Finally, two families have widely invaded the marine realm; interestingly, both groups include the only catfishes known from Australia. The eeltail catfishes, a rather small family of 27 species, is known from the Indian and the western Pacific Oceans and extends to Japan and Fiji. The sea catfishes (Ariidae) includes about 200 species in all the tropical continental shelves.

Habitat

Catfishes occupy practically all freshwater environments, where they are often the dominant group of fishes. Catfishes are mostly benthic and freshwater inhabitants, and they can be ubiquitous in the rivers of tropical continents such as South America and Asia, invading habitats such as riffles and waterfalls, as well as marginal, almost stagnant ponds. Some groups occupy the water column, swimming above the bottom. In those hovering catfishes some bizarre adaptations are noteworthy. Some sheatfishes and glass catfishes, for example, hover tail down, and both groups are schooling, transparent, with long barbels (one or four pairs), a long anal fin, a minute or absent adipose fin, a forked tail, and a dorsal fin completely lacking or represented by a sole reduced ray. Other catfishes, such as some banjo catfishes and most eeltail and sea catfishes, are estuarine and may venture even to deep-bottom continental-shelf environments or to offshore islands.

A bulldog pleco (*Chaetostoma sp.*) from the Amazon River in Brazil. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

An African polka-dot catfish (*Synodontis angelicus*) from the Zaire River in the Congo. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Behavior

Catfishes are generally bottom-dwelling, nocturnal, and solitary inhabitants of freshwater environments. However, an important minority are relatively specialized. For example, some sheatfishes, glass catfishes, and long-whiskered catfishes live far away from the bottom, are diurnally active, and may form schools. Eeltail catfishes and some thorny catfishes are well known for forming relatively large schools close to the bottom. Many South American species of armored catfishes are benthic and diurnal.

Feeding ecology and diet

Catfishes exhibit a wide array of feeding strategies. Most species live intimately linked to the bottom and feed mainly on invertebrates. Fish eaters are also abundant. For example, the squarehead, angler, and frogmouth catfishes (Chacidae) belong to a small group of Asian species that may use their maxillary barbels to attract smaller fishes to their enormous mouths. On the other hand, the Neotropical suckermouth armored catfishes (Loricariidae) are basically plant eaters, taking aquatic and terrestrial materials, such as algae and fallen leaves and trees. Catfishes, mainly those included in the pencil catfish family (Trichomycteridae), also engage in parasitic activities. Parasitic catfishes may be lepidophagous, targeting mucus, scales, and associated tissues (stegophyline trichomycterids), or hematophagous, swallowing blood (vandelliine trichomycterids). Some lepidophagous parasitic catfishes eat large pieces of flesh and enter the body cavities of their host. These species attack and devour commercially important catfishes trapped in nets or hooks and are therefore considered pests.

Catfishes are under the predatory pressure of almost all carnivores sharing their habitat. Even large predatory species are eaten as eggs, larvae, and juveniles. Their main fish predators are gars, bony tongues, trahiras, Nile perch, cichlids, and of course, other catfishes. Non-fish predators include crocodiles and caimans, and freshwater and coastal dolphins.

Schouteden's African squeaker catfish (*Synodontis schoutedeni*) from the Congo, West Africa. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

The usual process of catfish reproduction involves adult specimens with reduced or absent external sexual dimorphism and some courtship activity before the demersal spawning, followed by moderate engagement in parental care of the rather small eggs. Most guarding of eggs and fry is carried out by males. Nevertheless, females of some relatively large banjo catfish species, such as *Aspredinichthys tibicen* and *Aspredo aspredo*, manage to adhere the eggs after fertilization to spongy tentacles or cuplike depressions present seasonally on their bellies. It has been said that the mother nurtures the litter. Another highly derived system, brood parasitism, has been developed by a squeaker species, *Synodontis multipunctatus*, which could be referred to as an aquatic "cuckoo." This Lake Tanganyika mochokid shares its habitat with a mouth brooding species of Cichlidae. The catfish synchronizes its spawning activity to that of the cichlid, allowing the perciform female to ingest its eggs for mouth brooding. The process does not end when the squeaker eggs hatch. Since the squeaker eggs hatch before the cichlid eggs, the catfish fry feed upon the host's fry inside her mouth!

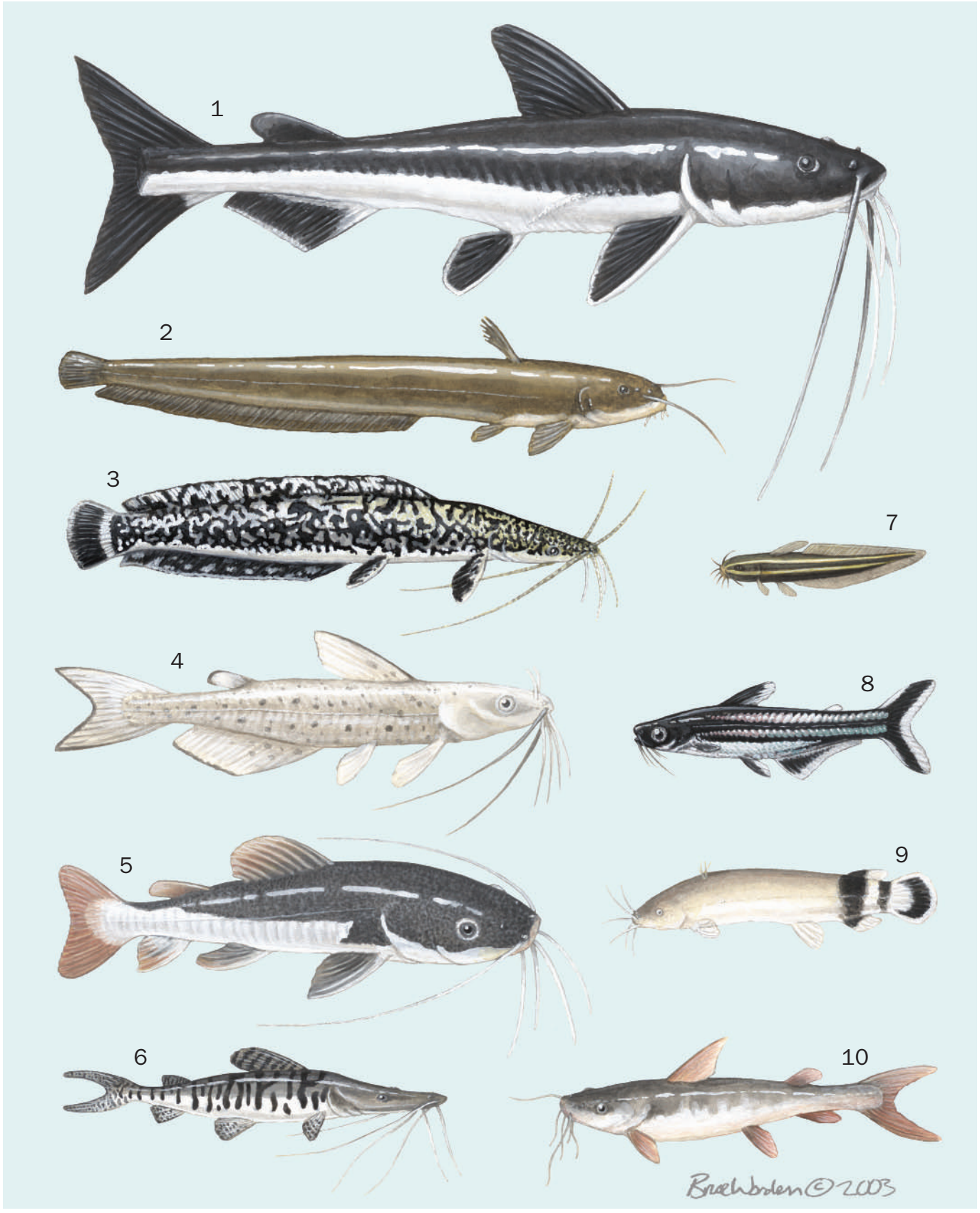
In many cases parental care by the male is highly significant. Perhaps the best example of this is the mouth-breeding sea catfish. Sea catfishes are relatively dimorphic: females develop pads or claspers on the pelvic fins and males shed the teeth on the roof of their mouth. The process by which the female transfers the fertilized eggs to the male's mouth is not clear. In any case, he fasts for as long as two months until the fry are released.

Conservation status

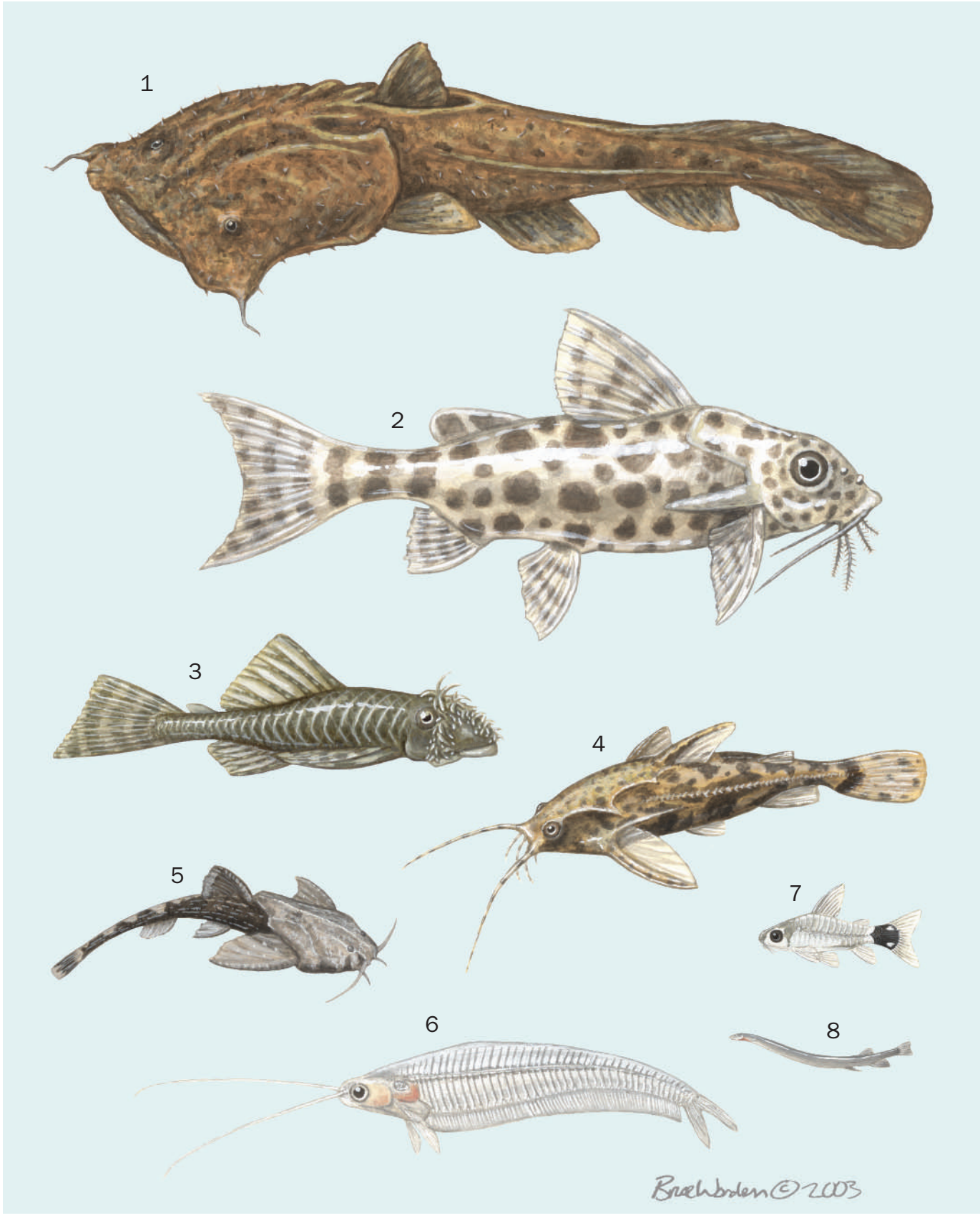
The IUCN Red List includes 66 siluriform species. One, the bagre graso (*Rhizosomichthys totae*), a pencil catfish from the Tota Lake, 9,845 ft (3,000 m) high in the Colombian Andes, is classified as Extinct. In addition, 8 species are listed as Critically Endangered; 7 as Endangered; 22 as Vulnerable; 4 as Lower Risk/Near Threatened; and 24 as Data Deficient.

Significance to humans

Catfishes are considered one of the more important orders of vertebrates, not only because more than one-tenth of living fishes are siluriforms, but because their relationship with humans covers many aspects of life and culture. Several hundred species are now used as food, and other species will be looked upon as a source of protein in the future. Some species are greatly appreciated as game and commercial fishes and reach high market prices, but some are simply the difference between starvation and survival for millions of humans. In addition, most catfishes can be used as aquarium fishes, a business that is not only worth millions of dollars, but gives urban populations the opportunity to get in touch with a significant part of nature.



1. Lau-lau (*Brachyplatystoma filamentosum*); 2. European wels (*Silurus glanis*); 3. Sharptooth catfish (*Clarias gariepinus*); 4. Channel catfish (*Ictalurus punctatus*); 5. Redtail catfish (*Phractocephalus hemioliopterus*); 6. Tiger shovelnose catfish (*Pseudoplatystoma fasciatum*); 7. Coral catfish (*Plotosus lineatus*); 8. Iridescent shark-catfish (*Pangasius hypophthalmus*); 9. Electric catfish (*Malapterurus electricus*); 10. New Granada sea catfish (*Ariopsis bonillai*). (Illustration by Bruce Worden)



1. Squarehead catfish (*Chaca chaca*); 2. Blotched upsidedown catfish (*Synodontis nigriventris*); 3. Branched bristlenose catfish (*Ancistrus triradiatus*); 4. Blue-eye catfish (*Amblydoras hancockii*); 5. Guitarrita (*Dysichthys coracoideus*); 6. Glass catfish (*Kryptopterus bicirrhis*); 7. Dwarf corydoras (*Corydoras hastatus*); 8. Candiru (*Vandellia cirrhosa*). (Illustration by Bruce Worden)

Species accounts

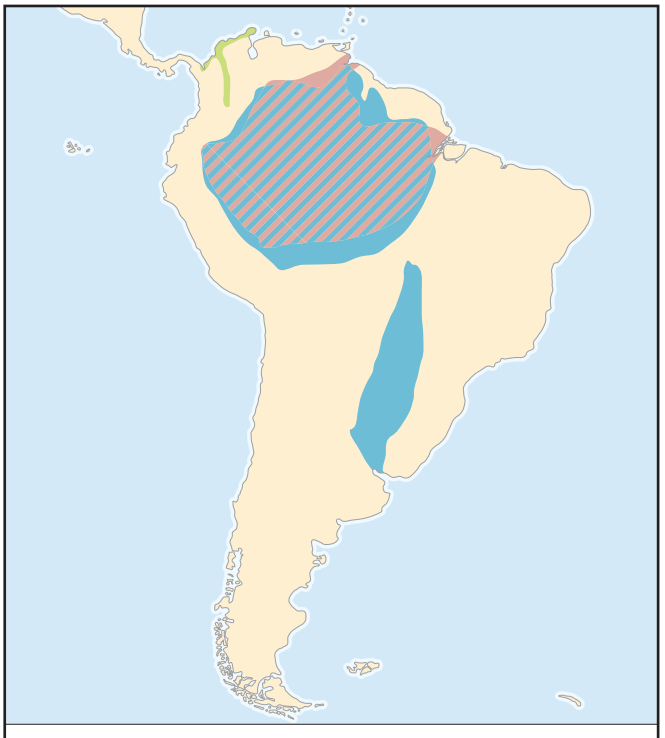
New Granada sea catfish
Ariopsis bonillai

FAMILY
Ariidae

TAXONOMY
Galeichthys bonillai Miles, 1945, Magdalena River, Honda, Colombia.

OTHER COMMON NAMES
French: Mâchoiron requin; Spanish: Chivo cabezón, chivo cazón.

PHYSICAL CHARACTERISTICS
Length 31.5 in (80 cm). Body naked, elongate, and robust; dorsal fin with one spine and seven soft rays; adipose fin present; pectoral fins with one spine and 10 soft rays; pelvic fins with six soft rays, inner rays strongly modified to form a hook in mature females; caudal fin deeply forked; head covered by a very rugose bony shield, well visible beneath the skin and extended anteriorly to opposite eyes, the posterior portion of the shield extends backward to meet the predorsal plate, which is large and crescent-shaped; three pairs of barbels; posterior pair of nostrils partly covered by a flap of skin; eye large, with free orbital rims. Dark gray to bluish gray dorsally, bluish white ventrally.



DISTRIBUTION
Southern Caribbean between Colombia and the Gulf of Venezuela.

HABITAT
Mainly inhabits coastal, brackish water, mangrove-lined lagoons, but has been collected in riverine environments as well as in shallow turbid marine waters.

BEHAVIOR
Benthic over muddy bottoms; solitary or forms schools.

FEEDING ECOLOGY AND DIET
Omnivorous; feeds mainly on benthic invertebrates, including crustaceans and polychaetes, but also consumes insects, small fishes, algae, and detritus.

REPRODUCTIVE BIOLOGY
As with all studied members of this family, engages in oral brooding; the male incubates the relatively large eggs in his mouth until hatching. Spawning occurs almost year round, with a peak in the Ciénaga Grande de Santa Marta between April and July. Fecundity is rather low, each female produces 24–39 eggs of about 0.5 in (1.3 cm). Sexual maturity is reached at sizes around 17 in (43 cm), but sexes can be told apart using external morphology at 7.5 in (19 cm). Males carry eggs and young for about two months.

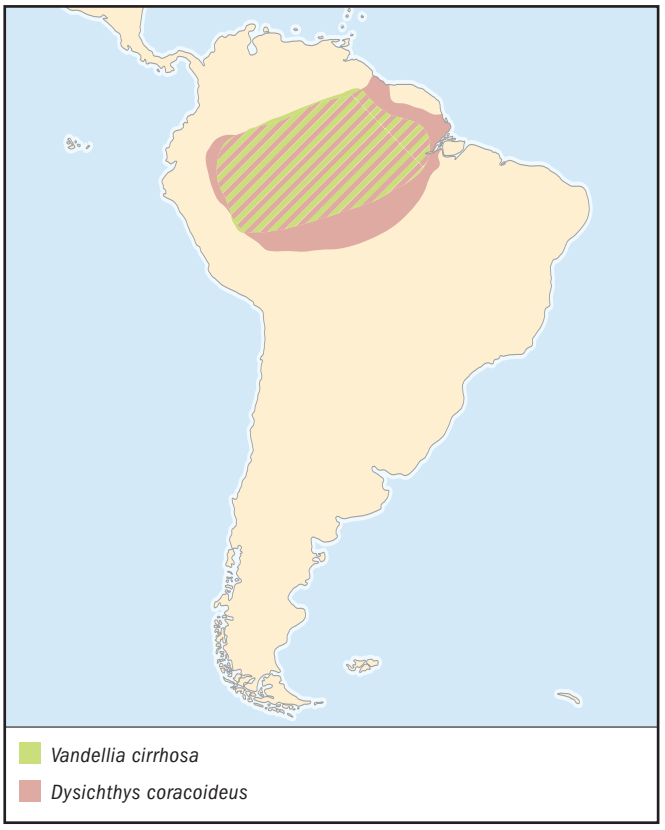
CONSERVATION STATUS
Classified as Endangered by the IUCN. This status is due to its endemicity to the southern Caribbean, combined with enormous pressure from artisan fisheries and significant habitat alteration. As a consequence of overfishing, the medium size of capture (12 in/30.5 cm) is well below the size of sexual maturity.

SIGNIFICANCE TO HUMANS
Fished for with hook and line, cast nets, and beach seines. Widely used as food by fishing communities and low-income populations of cities and towns in the Colombian Caribbean. By 2002 attempts to develop a specific aquaculture procedure were being made. Young may be used also as an aquarium species. ◆

Guitarrita
Dysichthys coracoideus

FAMILY
Aspredinidae

TAXONOMY
Dysichthys coracoideus Cope, 1874, Nauta, Peru. Nomenclatural situation is confused due to lack of clarity of the type species of genus *Bunocephalus*. Sometimes divided in two subspecies: *D. coracoideus coracoideus* for the Amazonas, and *D. coracoideus amaurus* for the Guyanas; the last subspecies may be treated as a separate species (*D. amaurus*) under the common name camouflaged catfish.



OTHER COMMON NAMES
English: Guitarrero, little guitar; French: Poisson banjo; Spanish: Catalina, guitarrita; Portuguese: Rabeca; Guyanas indigenous languages: Grongron, kronkron.

PHYSICAL CHARACTERISTICS
Length 4.3 in (11.0 cm). Body naked but covered by papillae or bumps; dorsal fin spineless, with five rays; adipose fin absent; anal fin short, with seven rays; pectoral fins with a strong serrated spine; caudal peduncle long and slender; caudal fin rounded; head and anterior part of body depressed; head covered by thickened bones; mouth small and anterior; three pairs of relatively short barbels; eyes small and on top of head; gill opening a short slit; anterior and posterior borders of pectoral fin spines with strong and recurved teeth.

DISTRIBUTION
South America in the Amazon River basin and Guyanas.

HABITAT
Fresh waters in ponds and small forest streams rich in plant remains.

BEHAVIOR
Bottom dwelling; swims by wavelike motion of body and tail; ejection of water through the gill slits results in a jerky forward movement.

FEEDING ECOLOGY AND DIET
Omnivorous, even feeds on organic matter from the bottom.

REPRODUCTIVE BIOLOGY
Spawns in groups; female does not carry her eggs, but lays 4,000–5,000 eggs each time on sandy bottom nests made by the male, which guards the eggs and fry.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Too small to be of interest as a food fish. However, it is an important aquarium fish which has been spawned in captivity. ◆

Dwarf corydoras
Corydoras hastatus

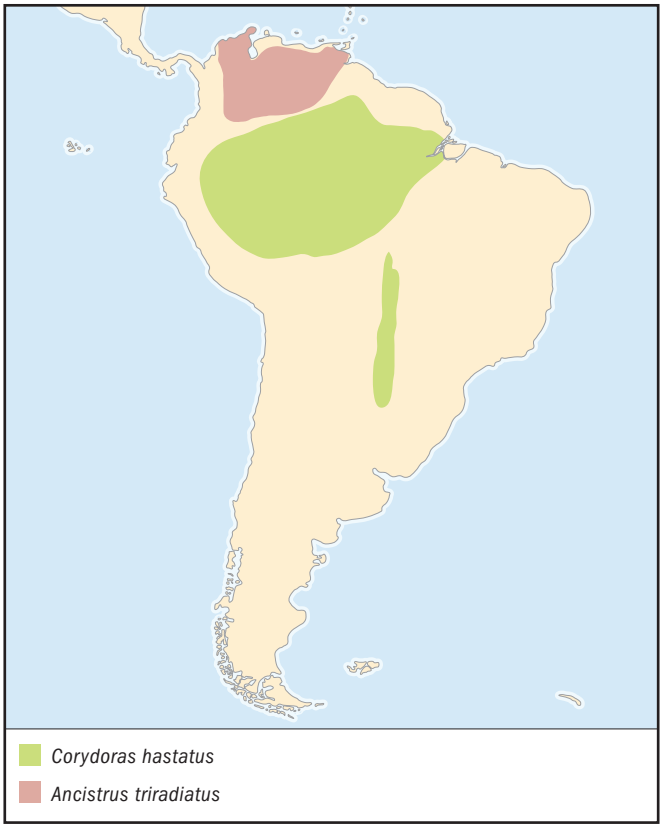
FAMILY
Callichthyidae

TAXONOMY
Corydoras hastatus Eigenmann and Eigenmann, 1888, Villa Bella (=Parintins), Amazonas, Brazil.

OTHER COMMON NAMES
English: Pygmy corydoras; French: Corydoras nain; Spanish: Coridoras enano, corredora.

PHYSICAL CHARACTERISTICS
Length 1.4 in (3.5 cm). Body compressed, with two rows of overlapping bony plates on each side, the nuchal scutes not meeting dorsally; dorsal fin with a strong spine and seven soft rays; spine at anterior border of adipose fin; pectoral fins with a strong spine and eight rays; caudal fin forked; head compressed; mouth small and ventral; two pairs of well-developed barbels.

DISTRIBUTION
South America in Amazon and Paraguay River basins.



HABITAT
Fresh waters in ponds.

BEHAVIOR
Forms small schools in midwater among aquatic vegetation. It rests on any kind of plant leaves in normal position or with the ventral surface up against the bottom of a leaf, high above the bottom. Normally swims by rapidly moving the pectoral fins, which, combined with a rapid breathing rate, gives it a rather nervous appearance.

FEEDING ECOLOGY AND DIET
Feeds among plants, as well as from the bottom, on small invertebrates and on detritus.

REPRODUCTIVE BIOLOGY
Sexually dimorphic; males are more elongate and their dorsal fins are more pointed. Near the time of spawning, both sexes clean their surroundings, mainly plant leaves. Courtship consists first of dashing about back and forth and up and down. Then the so-called "T" position is assumed close to the bottom; the female positions herself at the side of the male, close to his vent, pushing him with her head while constantly moving her barbels. After some "trembling" by both sexes, the female lays an egg. After fertilization the egg is carried in the female's ventral pouch and deposited over one of the leaves cleaned before. The female continues to spawn single eggs for one to two hours over three or four consecutive days. At this rate, a total of 30–60 eggs are spawned by each female. Since group spawning is normal, 300 eggs or more are frequently deposited. Fry 0.20 in (0.5 cm) long hatch usually after three to four days, and mature in about 200 days. The parents can spawn again after two weeks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Commercially important for the aquarium trade. ◆

Squarehead catfish
Chaca chaca

FAMILY
Chacidae

TAXONOMY
Platystacus chaca Hamilton, 1822, northeastern Bengal.

OTHER COMMON NAMES
English: Angler catfish, chaca, chega, Indian frog-mouth catfish; Spanish: Bagre cabezicuadrado.

PHYSICAL CHARACTERISTICS
Length 9.1 in (23 cm). Body compressed posteriorly; with many fine granulations; dorsal fin with a short spine and four soft rays; adipose fin a low ridge confluent with caudal fin; pectoral fin with one serrated spine and five soft rays; pelvic fins large, with six rays; a row of cirri above the lateral line; head broad and depressed, almost square, with a deep longitudinal groove located dorsally; mouth terminal, very wide, provided with appendages resembling barbels; three pairs of small barbels; eyes very small.

DISTRIBUTION
Asia in India, Bangladesh, and Nepal.

HABITAT
Freshwater; bottom dweller in rivers, canals, ponds, and flood plains.

BEHAVIOR
Prefers soft bottoms, where it hides lying still on the river bed. Depends completely on this concealment for protection, remaining motionless even after being touched.

FEEDING ECOLOGY AND DIET
Sometimes moves its tiny maxillary barbels in a jerky motion to lure small fishes, including gouramies and cyprinids, near its large mouth; may take fishes as large as one-half its length.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not listed by the IUCN.

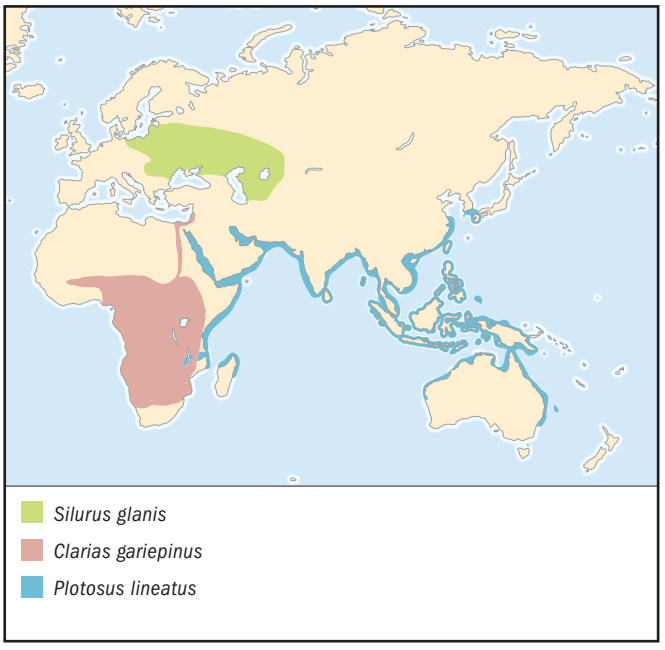
SIGNIFICANCE TO HUMANS
Commonly fished but not eaten probably due to its odd appearance. Sometimes used as an aquarium fish. The dorsal spine can inflict painful wounds if the fish is stepped on. ◆

Sharptooth catfish
Clarias gariepinus

FAMILY
Clariidae

TAXONOMY
Silurus (Heterobranchus) gariepinus Burchell, 1822, Smidtsdrift, Vaal River, Cape Province, South Africa.

OTHER COMMON NAMES
English: Mubondo, North African catfish, Zambezi barbel; Spanish: Bagre dientón.



PHYSICAL CHARACTERISTICS
Length 5.6 ft (1.7 m); weight 132 lb (60 kg). Body naked and elongate; dorsal fin base very long, with 61–80 rays, not preceded by a spine, not continuous with caudal fin; adipose fin absent; pectoral fin spine serrated only on its external border; anal fin long, separated from caudal fin; caudal fin rounded; head depressed, covered with rugose bony plates; mouth terminal and transverse; four pairs of barbels; eyes superior, relatively small, and with a free orbital rim; gill openings wide; air-breathing labyrinthic organ arising from second, third, and fourth gill arches. Coloration countershaded, dark gray dorsally, milky white ventrally, ventral surface of head in adults with a black longitudinal band in each side; band absent in juveniles.

DISTRIBUTION
Africa in Niger and Nile River basins; also the Limpopo, Orange-Vaal, Okavango, and Cunene Rivers, South Africa, and in the Middle East, including Israel, Jordan, Lebanon, and Syria.

HABITAT
Benthopelagic in fresh waters and upper estuaries 13–262 ft (4–80 m) deep, but more common in shallow environments.

BEHAVIOR
Widely resistant to challenging environmental conditions; the accessory labyrinthic organ allows clariid catfishes to breathe air under dry conditions. Favors shallow marginal areas, but may appear in the open; nocturnal. Capable of walking through dry land using tough pectoral fin spines. May also discharge electricity during intraspecific agonistic behavior.

FEEDING ECOLOGY AND DIET
Omnivorous bottom feeder, feeds on insects, fishes, crustaceans, mollusks, plankton, fruits, plants, small birds, and carrion. Occasionally feeds at the surface.

REPRODUCTIVE BIOLOGY
Migrates upstream or to lakeshores in large numbers to spawn immediately after the first heavy showers of the rainy season. Sexually dimorphic, both males and females have elongated sexual organs, but male organ has cone-shaped tip. Spawning is nocturnal in shallow waters; eggs, which have an adhesive disk and are less than 0.10 in (0.25 cm) long, are not protected. Eggs hatch in one or two days. Juveniles stay in shallow, protected waters for about six months, migrating downstream before their nursery area dries up.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Although of relatively minor importance for fisheries, this is a valuable aquaculture species, due to its hardiness, rapid growth, ease of feeding and handling, and flesh quality. Also considered a game fish. Widely introduced to almost all Africa, and to some European, Asian, and South American countries; negative ecological impact has been reported. Trade restricted in Germany. ◆

Blue-eye catfish
Amblydoras hancockii

FAMILY
Doradidae

TAXONOMY
Doras hancockii Valenciennes, 1840, Demerara, Guyana.

OTHER COMMON NAMES
English: False talking catfish, Hancock's amblydoras, purring catfish; Spanish: Bagre ojiazul; Portuguese: Quiri-quiri.

PHYSICAL CHARACTERISTICS
Length 5.9 in (15 cm). Body somewhat elongated, with a row of 24–28 lateral bony plates, each provided with a posteriorly directed hook; anterior granulations of body confluent into a large buckler; dorsal fin spine grooved, but lacking teeth, six dorsal soft rays; interdorsal plate absent; adipose fin present; pectoral fins' spines serrated on both edges, capable, as the dorsal spine, of being erected and locked; caudal fin truncated; head large and depressed; mouth terminal; three pairs of unbranched barbels; eye located in the middle of head. Dark brown to violet dorsally, white ventrally, a white strip along the body; eyes bright blue.

DISTRIBUTION
South America in Guyana and eastern Brazil to Peru and Bolivia.

HABITAT
Freshwater in coastal swamps, flood plains, ponds, and creeks.

BEHAVIOR
Lives in schools, sometimes by hundreds, hiding during the day in places with the bottom covered by plant material, mainly fallen trees and leaves. Resists desiccation by crawling to a suitable body of water. Can produce sounds by different combinations of pectoral spines, swim bladder, and the sophisticated internal elastic spring apparatus.

FEEDING ECOLOGY AND DIET
Nocturnal plant and detritus eater in the wild, but reported to eat animal material, such as worms, in captivity.

REPRODUCTIVE BIOLOGY
Spawns in the rainy season. The male builds a nest of bubbles, leaves, and other plant material at the surface, where the female lays the eggs in a flattened cluster. The male guards the nest until egg hatching.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not important to fisheries due to its small size. Commercially important as an aquarium fish. ◆

Channel catfish
Ictalurus punctatus

FAMILY
Ictaluridae

TAXONOMY
Silurus punctatus Rafinesque, 1818, Ohio River, United States.

OTHER COMMON NAMES
English: Blue channel catfish, eel catfish, fiddler, forked-tail cat, government cat, Mississippi cat, river cat, sand cat, sharpie, silver cat, speckled cat, spot, white cat, willow cat; Spanish: Bagre de canal.

PHYSICAL CHARACTERISTICS
Length 4.3 ft (1.32 m); weight 58 lb (26.3 kg). Body naked and elongate; dorsal fin with a spine and six or seven soft rays; adipose fin small, remote from caudal fin, which is deeply forked; pectoral fins with a spine with large posterior serrae; pelvic fins with eight soft rays; mouth subterminal to inferior; four pairs of barbels; eye large and oval. Young mottled, brownish above, whitish below; adults mainly deep slate brown.

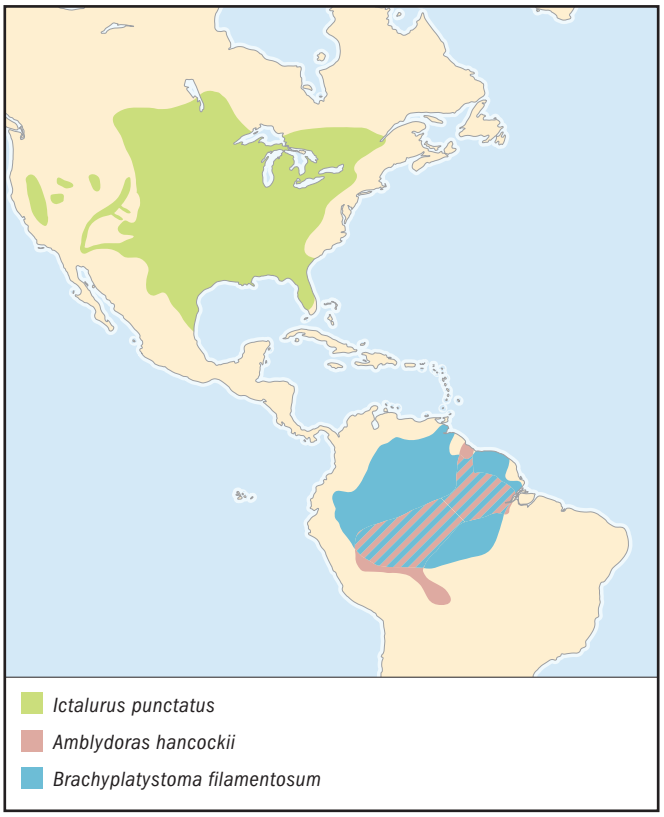
DISTRIBUTION
North America, native to central drainages of the United States and Mexico into southern Canada east of the Rocky Mountains, and possibly parts of the Atlantic coast. Original distribution somewhat unclear due to extensive introductions to the Atlantic coast and elsewhere. Fossils 10–20 million years old have been reported.

HABITAT
Freshwater in clear, well-oxygenated streams, and medium to large rivers with swift currents over relatively hard bottoms, including sand, gravel, and rocks. Also in quiet waters of lakes, reservoirs, and ponds. May enter brackish waters. Taken as deep as 49 ft (15 m).

BEHAVIOR
Benthic. Capable of relatively long migrations. Travels upstream in the spring and downstream in the fall. Young school close to the bottom at light hours during their first year, scattering at night.

FEEDING ECOLOGY AND DIET
A nocturnal carnivore, feeds mainly on small fishes, crustaceans, insects, and mollusks. Reported to also eat filamentous green algae. Well known for taking almost any bait, including rotten items.

REPRODUCTIVE BIOLOGY
Spawning occurs during the day in nests guarded by the male, beginning early spring in the south but later in the northern parts of its range, usually when the water warms to 60–75°F (16–24°C). Eggs hatch in 6–10 days. Maturity is reached in 2–5 years at about 1 ft (0.3 m) long. Reported to live 16 years.



CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Highly important fishery, aquaculture, aquarium, and game species. It is a top sport fish, and is actively farmed. Used in "pay as you fish" ponds. Mississippi produces over 90% of the channel catfish farm-raised in the United States. In 1996, Mississippi ponds produced 334 million lb (about 152 million kg) valued at $265 million. Trade is restricted in Germany, where it is considered a potential pest. ◆

Branched bristlenose catfish
Ancistrus triradiatus

FAMILY
Loricariidae

TAXONOMY
Ancistrus triradiatus Eigenmann, 1918, Quebrada Gramalote, Barrigona, Villavicencio, Departamento del Meta, Colombia.

OTHER COMMON NAMES
Spanish: Cucha barbuda.

PHYSICAL CHARACTERISTICS
Length 4.7 in (12 cm). Body broad and depressed, covered with bony plates, 23–26 in the lower lateral series; belly naked; dorsal fin with one spine and eight rays; adipose fin present, not attached to adipose fin by a membrane; caudal fin truncate; anal fin with one spine and three to four rays; pectoral fin spine short, not reaching the origin of pelvic fin; anterior

portion of upper snout surface naked and with well-developed branching barbels in males, barbels small and simple in females; mouth ventral; teeth small, numerous, and bifid; opercular bones armed with about a dozen spines.

DISTRIBUTION
South America in middle and lower Orinoco River tributaries; Venezuelan and Colombian Caribbean coastal drainages, including the Magdalena River; Lake Maracaibo Basin, including the Catatumbo River.

HABITAT
Fresh waters. Benthic, in fast-running mountain streams with coarse pebble bottoms; lives as high up as 3,300 ft (1,000 m).

BEHAVIOR
Relatively shy fishes, usually live in caves or below rocks.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds on filamentous algae and microorganisms growing on rocks, logs, and leaves. Also rasps rotten wood and ingests the cellulose. The lignin is reportedly important for their digestive processes.

REPRODUCTIVE BIOLOGY
The male selects an area such as under a log or a rocky cave and after some hours of courtship the female lays 50–150 yellowish to orange eggs, about 0.10 in (2.5 mm) long, which are guarded by the male and hatch in one week or less.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Unimportant for fisheries. Used as an aquarium fish, it has been spawned in captivity. ◆

Electric catfish
Malapterurus electricus

FAMILY
Malapteruridae

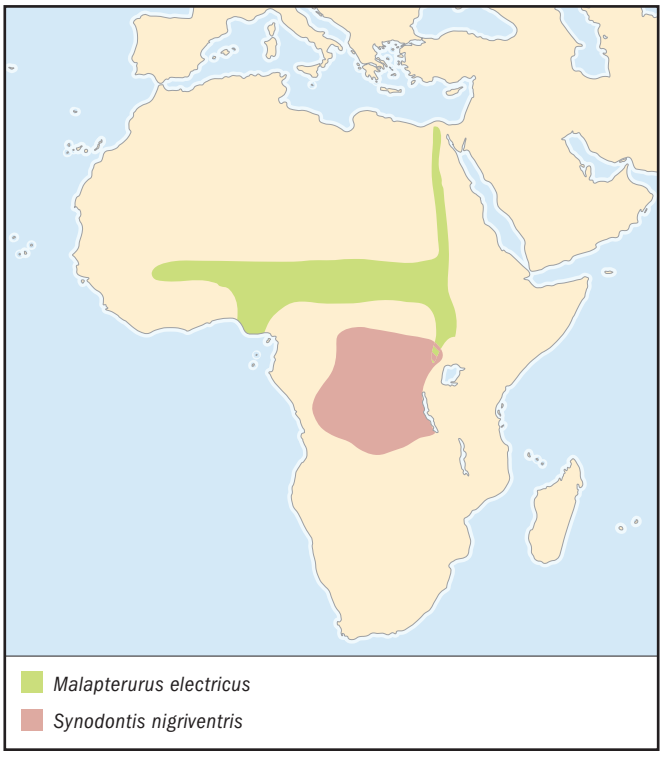
TAXONOMY
Silurus electricus Gmelin, 1789, Rosetta, Nile River.

OTHER COMMON NAMES
French: Silure éléctrique; Spanish: Bagre eléctrico.

PHYSICAL CHARACTERISTICS
Length 4 ft (1.22 m); weight 59.5 lb (27 kg). Body naked and sausage-shaped; a thick subdermal electrogenic organ derived from pectoral musculature extends the entire length and circumference of the fish; dorsal fin absent; adipose and anal fins far back; pectoral fin spine absent; swim bladder with an elongate posterior chamber; caudal fin rounded; mouth terminal; three pairs of long and fleshy barbels; eyes small and without a free border. Very large spots on the body and vertical bars on posterior part of the body and caudal fin.

DISTRIBUTION
Africa in Nile, Chad, and Niger basins.

HABITAT
Benthic in freshwater.



BEHAVIOR
Rests around rocks and roots in quiet waters during the day, becoming active at night. Intermittently produces electric discharges of basically two types: high frequency, used for self-defense and prey capture, and low frequency, associated with prey detection. Discharges can be 100–400 V, depending on catfish size. Generally, the initial shock, short and sharp, is followed by less intense secondary discharges.

FEEDING ECOLOGY AND DIET
A poor swimmer, feeds mainly on aquatic invertebrates and small fishes stunned by its electric discharges. Food items reported from stomachs are shrimps and fishes, such as cichlids, clupeids, schilbeids, bagrids, cyprinids, and characids.

REPRODUCTIVE BIOLOGY
Forms pairs during the rainy season; spawning occurs in excavated holes. Reported to live 10 years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Used in subsistence fisheries and considered a game fish; also important for show aquariums. However, it is better known for its strong electric discharges, which are supposed to be capable of knocking down a person if the catfish is stepped on. Humans have known about these electric capabilities for over 5,000 years. ◆

Blotched upsidedown catfish
Synodontis nigriventris

FAMILY
Mochokidae

TAXONOMY
Synodontis nigriventris David, 1936, Buta, Congo Democratic Republic (=Zaire).

OTHER COMMON NAMES
Spanish: Bagre manchado al revés.

PHYSICAL CHARACTERISTICS
Length 3.8 in (9.6 cm). Body naked and relatively elongated; dorsal and pectoral fin spines strong and with a locking mechanism; adipose fin very large, not rayed; caudal fin forked; head bony, with a nape shield; mouth relatively small, lips not suckerlike; three pairs of barbels, mandibular barbels branched, eye with a free border. Color reverse countershaded, dorsal surface light, ventral surface dark.

DISTRIBUTION
Africa in Central Congo basin.

HABITAT
Benthopelagic in fresh water.

BEHAVIOR
Schools by the thousands. Large fishes swim upside down and may be able to escape predation by hiding with the ventral surface up under a log. Young swim in a conventional way. The pectoral fin spine produces a squeaking sound when it moves in its socket.

FEEDING ECOLOGY AND DIET
Nocturnal. Uses its inverted swimming position to feed on filamentous algae that grow on cave ceilings and on the undersides of leaves and other aquatic vegetation, and also to take terrestrial insects and other material from the water surface. Also feeds on bottom material, such as plant and fish remains, crustaceans, and insect larvae.

REPRODUCTIVE BIOLOGY
Females lay about 100 eggs under a rock or on the roof of a cave; eggs hatch in about seven days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Unimportant for fisheries because of its small size. A widely used aquarium fish, has been spawned in captivity. ◆

Iridescent shark-catfish
Pangasius hypophthalmus

FAMILY
Pangasiidae

TAXONOMY
Helicophagus hypophthalmus Sauvage, 1878, Laos.

OTHER COMMON NAMES
English: Candy-striped catfish, sutchi catfish, sharkfin catfish, silver catfish, swai; Spanish: Bagre sutchi.

PHYSICAL CHARACTERISTICS
Length 4.3 ft (1.3 m); weight 34 lb (15.5 kg). Body naked, compressed; predorsal area relatively keeled; dorsal fin far forward, with a sharp serrated spine and six soft rays; adipose fin small; anal fin long, with about 30–40 rays; pectoral fins with a sharp spine; caudal fin forked; head covered by soft skin; mouth small, subterminal; two pairs of barbels (maxillary and mandibular) that shorten with age; eyes above and below the corner of the mouth with a free orbital rim. Young with two black stripes, one along the lateral line and another below it; adults mainly gray.

DISTRIBUTION
Southeast Asia (Indochina) in Mekong and Chao Phraya basins. Introduced into streams for aquaculture.

HABITAT
Freshwater in large rivers.

BEHAVIOR
Benthic. Undergoes long upstream migrations, both reproductive and trophic, in late fall and early winter, migrates downstream in late spring and summer. Reported to be always on the move when in confinement; capable of sound production.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds on fishes, crustaceans, mollusks, and plant litter. Young tend to be carnivorous, eating more plants while growing.

REPRODUCTIVE BIOLOGY
Since eggs appear from March to August, it is believed that the downstream migration is not only trophic, but also reproductive.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Important commercially for fisheries, aquaculture, and the aquarium trade. ◆

Lau-lau
Brachyplatystoma filamentosum

FAMILY
Pimelodidae

TAXONOMY
Pimelodus filamentosus Lichtenstein, 1819, Brazil.

OTHER COMMON NAMES
French: Torch; Spanish: Lechero, plumita, valentón, zungaro saltón; Portuguese: Filhote, piraíba, piratinga; Guyanas indigenous languages: Axakwan, lektaima, pilau.

PHYSICAL CHARACTERISTICS
Length 11.8 ft (3.6 m); weight 440 lb (200 kg). Body naked; dorsal and pectoral fins with one spine; adipose fin long based; caudal fin deeply forked, upper and lower fin rays very long; head broad; snout very depressed; mouth slightly ventral; maxillary barbels very long, one to two times the length of the body in juveniles, two-thirds the length of the body in adults; eyes small, dorsolaterally located, with a free orbital rim. Color dark gray dorsally, whitish ventrally.

DISTRIBUTION
South America in Amazon and Orinoco basins, also main rivers of the Guyanas and northeastern Brazil.

HABITAT
Channels of large rivers, including muddy, black-water and clear-water tributaries, and upper reaches of estuaries. Young specimens occur in flood plains and ponds as well as on the main river channels and even in brackish water.

BEHAVIOR
Soft-bottom dweller, but a good swimmer capable of long migrations.

FEEDING ECOLOGY AND DIET
Piscivorous, mainly consuming characids, catfishes, and knifefishes it swallows whole. Monkeys have also been reported from the stomachs of large specimens.

REPRODUCTIVE BIOLOGY
Medium sizes at maturity in the lower Caquetá (=Japurá) river are 59 in (1.5 m) standard length for females, 51 in (1.3 m) for males. Estimations of fecundity are variable, figures range from 60,000 eggs for a 143 lb (65 kg) specimen to one million eggs for a 106 lb (48 kg) female. Spawning in Venezuela coincides with the rainy season; young specimens are found in July and August.

CONSERVATION STATUS
Not listed by the IUCN. However, it is considered endangered in Colombia due to overfishing, and most specimens fished at the turn of the twentieth century in that South American country were immature. Minimum legal capture size in Colombia is 40 in (1 m).

SIGNIFICANCE TO HUMANS
Highly important commercial fish captured using nets and longlines, flesh is considered of excellent quality. Also a valuable game fish. Older literature reports that lau-lau occasionally prey on humans. ◆

Redtail catfish
Phractocephalus hemioliopterus

FAMILY
Pimelodidae

TAXONOMY
Silurus hemioliopterus Bloch and Schneider, 1801, Maranham River, Brazil.

OTHER COMMON NAMES
Spanish: Bagre colirrojo, guacamayo, pez torre; Portuguese: Bigorilo, guacamayo, peixe-arara, pirarara.

PHYSICAL CHARACTERISTICS
Length 4.4 ft (1.34 m); weight at least to 176.2 lb (80 kg). Body stout and naked; dorsal fin with one spine and seven rays; adipose fin short and high; caudal fin broad and almost square; head as broad as high, flattened dorsally; maxillary barbels extending at least to dorsal fin level; eyes small, with free margins; nostrils widely separated; pectoral fins spine thick with sharp, recurved teeth posteriorly. Coloration countershaded, vertical fins with bright orange tips, white ventrally.

DISTRIBUTION
South America in Amazon and Orinoco River basins. Reported from Venezuelan fossils six million years old.

HABITAT
Freshwater.

BEHAVIOR
Bottom dwelling. In the upper Caquetá River (Colombia) its upstream migration occurs between March and June.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds on animals (fishes and crabs) and plant material (fruits).

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Important for subsistence fisheries, also a game fish. Commercially important as an aquarium fish; introduced, but not established, in Florida. ◆

Tiger shovelnose catfish
Pseudoplatystoma fasciatum

FAMILY
Pimelodidae

TAXONOMY
Silurus fasciatus Linnaeus, 1766, Brazil, Suriname. The population restricted to the Magdalena-Cauca basin (Colombia), usually included under this name, seems to deserve status as a species.

OTHER COMMON NAMES
English: Tiger catfish, bared sorubim, tumare; French (Creole): Poson-tig, torch-tig; Spanish: Bagre pintadillo, bagre rayado, bagre tigre, zungaro doncella; Portuguese: Pintado, surubim, surubim-lenha.

PHYSICAL CHARACTERISTICS
Length 3.4 ft (1.05 m); weight 154.2 lb (70 kg). Body naked; dorsal and pectoral fin spines well developed and covered by thick skin; well-developed adipose fin; caudal fin forked; head large and depressed; upper jaw overhanging the lower jaw; maxillary barbels relatively short, not extending to anal fin; eyes relatively small and dorsally located; dorsal skull fontanel relatively short and shallow. Coloration dark gray dorsally, whitish ventrally, crossed by dark bands or loops.

DISTRIBUTION
South America in Amazon, Corintijns, Essequibo, Orinoco, and Paraná River basins.

HABITAT
Fresh waters in lakes, flooded plains, and forests, main river channels, and floating meadows. Absent from estuaries. Occurs at maximum depth of 16 ft (4.9 m).

BEHAVIOR
Bottom dweller. Strongly migratory. In the Amazon basin, undergoes two annual migrations: a feeding one in the dry

season and another at the beginning of the rainy season. In Venezuela, follows the migratory pattern of the bocachicos (Prochilodontidae) and other nomadic fishes.

FEEDING ECOLOGY AND DIET
Basically a nocturnal fish eater, consumes mainly characiform fishes, as well as other catfishes and cichlids, which it swallows whole. In the Apure River (Venezuela), 34 species of migratory fishes have been found in stomach contents. Spiders, crabs, and seeds are also taken.

REPRODUCTIVE BIOLOGY
Reproductive season in the Orinoco basin runs between March and June. Median sizes of gonad maturity in eastern Colombia estimated at 32.7 in (83 cm) standard length for females, and 23.6–41.3 in (60–105 cm) for males; relative fecundity was estimated as well as about 30,000 eggs per pound (about 60,000 per kg). Sizes at first sexual maturation reported as 22 in (56 cm) for females and 17.7 in (45 cm) for males.

CONSERVATION STATUS
Not listed by the IUCN. However, it is considered threatened in Colombia. The population from the Magdalena-Cauca basin is considered critically endangered. That country has tried to regulate the exploitation of the barred sorubim, as well as that of the northern Colombian population, establishing minimum sizes of capture and fishing seasons.

SIGNIFICANCE TO HUMANS
Enormously important for commercial fisheries in most countries where it occurs because of its excellent tasting yellowish flesh. Cultured in Colombia and Venezuela. Also a game fish and traded for show aquariums. ◆

Coral catfish
Plotosus lineatus

FAMILY
Plotosidae

TAXONOMY
Silurus lineatus Thunberg, 1787, Indian Ocean.

OTHER COMMON NAMES
English: Bumblebee catfish, striped eel-catfish; Spanish: Bagre-anguila rayado; Afrikaans: Streep-baberpaling.

PHYSICAL CHARACTERISTICS
Length 12.6 in (32 cm). Body naked, eel-like; dorsal fin short, with a sharp, highly venomous, spine armed with relatively small teeth on both borders, and four rays; no adipose fin; pectoral fins spines serrated and highly venomous; tail pointed, caudodorsal fin rays extending forward ahead of midbody, lower caudal rays joining the long anal fin, forming a continuous fin with 139–200 rays; lateral line fully developed; dendritic organs present behind vent; mouth transverse; four pairs of relatively short barbels; eye relatively small with free orbital margins. Young black with two or three white or yellow stripes, adults mainly gray brown.

DISTRIBUTION
Indian and western Pacific Oceans, from the Red Sea and East Africa, including Madagascar, to Samoa, southern Japan and Korea, Australia, Lord Howe, Palau and Yap Islands.

HABITAT
Marine. The only catfish observed in coral reefs, also in tide pools, brackish environments, and freshwater; bottom dweller to about 200 ft (61 m) deep.

BEHAVIOR
Solitary or forms tight shoals of hundreds in shallow water and tide pools, sometimes covering the bottom; schools may break into smaller pods that move coordinately. Schooling confuses and discourages predators.

FEEDING ECOLOGY AND DIET
Eats mainly invertebrates, such as crustaceans, mollusks, and worms, and fishes taken from the soft bottoms.

REPRODUCTIVE BIOLOGY
Oviparous; the eggs are spherical, a little larger than 0.10 in (0.25 cm), nonadhesive, demersal; larvae are planktonic. In Japan reproduction occurs in early summer, the male builds and guards a nest with debris and rocks where the female deposits her eggs; the eggs hatch in 10 days or less. Females reach maturity in about one year, at a length of 5.5 in (14 cm). Maximum reported age is seven years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The venomous fin spines are very dangerous (but rarely fatal); therefore all users of coastal waters, including bathers, swimmers, divers, and fishermen should be very cautious. Pectoral fin spines receive venom from the axillary and pectoral spine glands. Nevertheless, these fishes are used as food, mainly in Africa, and as aquarium fishes; in Japan they are kept and spawned in public and private aquaria. ◆

Glass catfish
Kryptopterus bicirrhis

FAMILY
Siluridae

TAXONOMY
Silurus bicirrhis Valenciennes, 1840, Java, Indonesia.

OTHER COMMON NAMES
English: Phantom glass catfish; Spanish: Bagre vítreo.

PHYSICAL CHARACTERISTICS
Length 5.9 in (15 cm). Body naked, strongly compressed; dorsal profile arched with a nuchal concavity; dorsal fin rudimentary, represented by only one short ray; adipose fin absent; anal fin base very elongate, with 55–68 rays; pectoral fins longer than head; pelvic fins small; caudal fin forked; mouth very small, oblique; one pair of barbels on lower jaw, maxillary barbels elongate, reaching to the anal fin; eye large, subcutaneous. Body translucent, internal features such as blood vessels and backbone visible, gut covered by a silvery peritoneum; depending on light the body may reflect iridescent colors, ranging from yellow to violet, or even fluorescent blue in twilight.

DISTRIBUTION
Asia in Mekong, Chao Phraya and Xe Bangfai basins, Malay Peninsula, Java, Sumatra, and Borneo.

HABITAT
Freshwater. Benthopelagic in large rivers and flooded plains, favors turbid shady waters.

BEHAVIOR
Free-swimming, shoaling species. In captivity, the group stays in a dark corner during light hours, only disturbed by individuals changing places.

FEEDING ECOLOGY AND DIET
A diurnal carnivore, feeds on pelagic and planktonic invertebrates, such as hemipterans, other insects, worms, and crustaceans, and small fishes. In captivity only takes floating items, it never disturbs the bottom looking for food.

REPRODUCTIVE BIOLOGY
Has not been spawned in captivity. No information from the wild.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An important aquarium species. Also used to make the fish sauce *prahoc.* ◆

European wels
Silurus glanis

FAMILY
Siluridae

TAXONOMY
Silurus glanis Linnaeus, 1758, Orient, European lakes.

OTHER COMMON NAMES
English: Catfish, Danube catfish, European catfish, sheatfish; German: Wels; French: Silure glane; Spanish: Bagre europeo.

PHYSICAL CHARACTERISTICS
Length 16.5 ft (5 m); weight 726 lb (330 kg). Body naked, robust, anteriorly compressed; dorsal fin with 1 spine and 4–5 rays; adipose fin absent; anal fin base very elongate, with 90–95 rays covered by integument for most of their length; pectoral fin spine stout; pectoral and pelvic fins short; caudal fin rounded; head broad and depressed; mouth terminal; maxillary barbels heavy, flattened.

DISTRIBUTION
Eurasia, including Baltic, Black, and Aral Seas estuaries.

HABITAT
Fresh and brackish waters, including quiet, shallow places such as marshes, lagoons, backwaters, and large lakes, and as deep as 98 ft (30 m) in large rivers and dams.

BEHAVIOR
Benthic, occurring mainly over mud and sandy bottoms, where it hides in holes and under logs or tree roots during day hours; active during the night. Considered nonmigratory; however, in the Baltic Sea it reportedly undergoes short spawning migrations upriver, returning to spend winter months in deeper waters close to the river mouth.

FEEDING ECOLOGY AND DIET
Nocturnal and highly carnivorous, feeds on almost any aquatic animal. Juveniles consume bottom-living invertebrates; adults ingest large crustaceans, fishes, amphibians, ducks and other birds, as well as water voles and other small mammals.

REPRODUCTIVE BIOLOGY
Spawning takes place in shallow lakes and on flooded areas during warm seasons, and even in saltwater in the Aral Sea. No nest building activity, but males do protect the adhesive eggs, 0.10 in (0.25 cm) each, which stick to aquatic vegetation or to large pieces of detritus, sometimes in numbers over 100,000. Hatching occurs in about 20 days. Reported to live 30 years.

CONSERVATION STATUS
Not listed by the IUCN; however, it appears in Appendix III of the Bern Convention (protected fauna). Considered a potential pest that produces a negative ecological impact when introduced, but it does not always become well established after transplantation.

SIGNIFICANCE TO HUMANS
Important commercial and sport fish throughout its range. Marketed fresh, canned, and frozen. An industry based on this species in eastern Europe and in countries of the former Soviet Union produces leather from the skin, glue from the gas bladder and bones, and cheap caviar from the eggs. ◆

Candiru
Vandellia cirrhosa

FAMILY
Trichomycteridae

TAXONOMY
Vandellia cirrhosa Valenciennes, 1846, probably South America.

OTHER COMMON NAMES
Spanish: Candirú.

PHYSICAL CHARACTERISTICS
Length 1 in (2.5 cm). Body naked and very elongate; dorsal fin short, without a pungent spine, its origin posterior to pelvic fins; adipose fin absent; anal fin origin behind dorsal fin base, short; mouth narrow and suckerlike, inferiorly located; lower jaw toothless; mental barbels absent; eyes without free margins; opercular bones with spines. With a yellowish tinge or almost transparent.

DISTRIBUTION
South America in the Amazon River basin.

HABITAT
Freshwaters. Benthic, burrows in sandy bottoms.

BEHAVIOR
Parasitic, enters the gill cavity of larger fishes, frequently long-whiskered catfishes, to suck blood.

FEEDING ECOLOGY AND DIET
An obligate parasite that in captivity refuses any kind of food. However, it attacks a living fish by entering the gill chamber when inhaled water is expelled. Once in place, the candiru lodges itself using its opercular spines, bites off tips of host's gill filaments, and gorges with flowing blood. The candiru's body can distend considerably, and after few minutes of feeding it drops off to the bottom, where it burrows or just remains quiet.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Known to enter the urogenital openings of bathers, usually if they happen to urinate under water. The candiru swims up the flow of urine, possibly mistaking it for the water flow from a gill cavity. After penetrating as far as possible, the fish locks its opercular spines into position. This has obviously serious consequences for both the fish and the person, since the candiru can only be removed by surgery. Humans in its range protect themselves by wearing tight clothing when swimming (and by refraining from urinating underwater). ◆

Resources

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Gymnotiformes

(South American knifefishes and electric eels)

Class Actinopterygii
Order Gymnotiformes
Number of families 5

Photo: A group of blackspot green knifefish (*Eigenmannia* sp.). (Photo by Wally and Burkard Kahl. Reproduced by permission.)

Evolution and systematics

South American freshwaters are dominated by fishes in the superorder Ostariophysi: the siluriforms, characiforms, and gymnotiforms together comprise more than 75% of all the known freshwater species in South America. Recent data based on cladistic methodology strongly indicate that Gymnotiformes and Siluriformes are sister groups within the Ostariophysi. Of the three Neotropical ostariophysan orders, the gymnotiforms have the smallest number of species. It is also the least investigated group as far as systematics and ecology are concerned. This is largely because many species are difficult to distinguish, hard to catch, especially in their preferred deep riverine benthic habitats, and finally yet importantly are of little commercial interest. The first known gymnotiform fish, now known as *Gymnotus carapo*, was described in 1648. In 1758 Linnaeus described four species, today known as *Electrophorus electricus*, *Gymnotus carapo*, *Rhamphichthys rostratus*, and *Apteronotus albifrons*. Our main understanding of the systematics of these fishes is based on work performed during the past 20 years. Science now recognizes 105 described and at least 32 undescribed species, grouped within 29 genera and 5 families. The family Gymnotidae includes 17 described species, the family Rhamphichthyidae 13, and the family Hypopomidae 15 species. The fishes of these families have retained the plesiomorphic pulse-type electric organ discharge. Twenty-four species are grouped in the family Sternopygidae and 43 in the family Apteronotidae; these knifefishes produce the derived tone-type electric organ discharge.

Sternopygus astrabes most closely resembles the ancestral gymnotiform phenotype. Gayet and Meunier in 1991 described the first fossil gymnotiform fish, *Ellisella kirschbaumi*, from the Upper Miocene (about 10 million years ago) from Bolivia. However, the morphological characteristics of *E. kirschbaumi*—the absence of dorsal and pelvic fins and the replacement of the caudal fin by a long bony cartilaginous rod (as seen in sternopygids) in the regenerated caudal part—indicate that knifefishes are much older than 10 million years.

Physical characteristics

The Gymnotiformes constitute a group of rather specialized fishes. In most species, the body is compressed laterally, very elongated and slender, with long caudal appendages and a long anal fin tht resembles a knife (thus the name knifefishes). The fishes lack pelvic and dorsal fins; the dorsal filament of the Apteronotidae is sometimes interpreted as a rudiment of an adipose fin, but it might also be modified muscle. The caudal fin is replaced by the caudal appendage except in the apteronotids, which possess a reduced caudal fin that is interpreted by some authors as being derived from the caudal appendage and not representing an intermediate state in the loss of a caudal fin. All gymnotiform fishes possess an extremely well-developed ability to regenerate the caudal, or hind, parts of their bodies. In the apteronotids, however, this feature is less pronounced.

The caudal appendage represents an extension at the end of the anal fin, including the axial skeleton (a bony rod in most cases), the spinal cord, the remaining soft tissues, and the electric organ. A derived feature of gymnotiform fishes is their head morphology, which apparently reflects an adaptation for specialized feeding. For example, some knifefishes possess large mouths (*Gymnotus*, some *Apteronotus*) and feed on large prey; some possess terminal mouths (*Rhabdolichops*, *Eigenmannia*) and feed on insect larvae and on plankton; some posses external teeth (*Oedemognathus*) and feed on scales; some posses a long curved mouth (*Sternarchorhynchus*) and search

Electric eels (*Electrophorus electricus*) live the Orinoco River and in rivers throughout the Amazon Basin. (Photo by Richard T. Nowitz/ Baltimore MD National Aquarium/Photo Researchers, Inc. Reproduced by permission.)

for insect larvae in holes and crevices. The same variations in head morphology, related to feeding, are found in the African mormyrid fishes.

The most outstanding feature of the knifefishes is the possession of electroreceptors and electric organs in the skin. In some *Rhabdolichops* species, the large transparent electric cells in the tail region can be easily seen by external inspection. *Electrophorus electricus* is characterized by strong electric discharges up to 700 volts (V) at more than 1 ampere, or amp (A); in addition, this species can emit weakly electrical discharges for orientation. All the remaining knifefishes produce weakly electrical discharges around 1 V. The electric organs are derived from muscle, except in apteronotids, where modified spinal axons constitute the electric organ. Some species, such as *Steatogenys elegans* and *Hypopygus lepturus*, possess accessory electric organs in the head region. Larvae of some species (families Sternopygidae, Apteronotidae) differentiate larval electric organs early during their development.

Distribution

Gymnotiform fishes occur in all Neotropical river systems, from the Rio Salado in the pampas of Argentina to the Rio San Nicolas of Chiapas in Mexico. Species diversity is highest in the Amazon river system (89 species), followed by the Orinoco river system (61 species), rivers found in the Guyanas (35 species), and the Parana-Paraguay river system (26 species). Fourteen species occur in northwestern South America, twelve in southeastern Brazil and in Uruguay, nine in northeastern Brazil, seven on the Pacific slope of South America, seven in Central America, and just one species in the Rio Sali-Dulce of northwestern Argentina and on the island of Trinidad.

Largely because of their poorly understood systematics, the distribution of gymnotiforms at the species level is not well known. The most widely distributed species seem to be *Gymnotus carapo*, *Brachyhypopomus pinnicaudatus*, *Apteronotus albifrons*, *Eigenmannia lineata*, and *Sternopygus macrurus*. Not surprisingly, these are the species most commonly encountered in the tropical fish trade.

Habitat

Most rivers in tropical South America can be classified according to water conditions: white water (e.g., the Amazon), black water (e.g., the Rio Negro) or clear water (e.g., the Rio Tapachos). All three types are characterized by low pH values (from 7 down to 3.5) and low levels of salts and nutrients. The freshwater systems of Central America have higher levels of mineral content due to their different geology. Gymnotiform fishes occur in all three major water types. In the extremely acidic and nutrient-poor black waters of the Rio Negro, 36 gymnotiform species have been found. Knifefishes occur in small streams, large rivers, lakes, and various types of backwaters. The enormous abundance of gymnotiforms that occur in deep, main-river channels was only recently discovered (1980s): in the Orinoco River system, for example, 86% of the fish species are gymnotiforms. It is still not well understood why this predominance occurs in this type of habitat.

Some knifefishes show adaptations to habitats with low oxygen. The electric eel (*Electrophorus electricus*; modified buccal cavity) and the banded knifefish (*Gymnotus carapo*; swim bladder) can take air from the water surface, as can several species of *Brachyhypopomus.* The electric eel is an obligatory air breather and drowns if denied access to atmospheric air. However, as long as its skin is kept moist, it can survive for several hours out of water. A large embryonic fin fold of the gymnotiform free embryos serves as a respiratory organ during early development.

Most gymnotiform fishes tolerate temperatures between 68 and 92°F (20 and 35°C); a few species, however, have been found in colder waters. *Apteronotus* sp. and the glass knifefish (*Eigenmannia lineata*) occurred in considerable quantities in the Huallaga River (about 64.4°F or 18°C in the tropical mountain rainforest near Tingo Maria, Peru). Under experimental conditions, *Sternarchorhynchus* sp. did not survive below 77°F (25°C), but tolerated temperatures up to 98.6°F (37°C). For *Sternopygus* sp., the range was 66.2–86°F (19–30°C).

In the field, gymnotiforms can tolerate pH values of 7 (Amazon) to below 4 (black water). In captivity, the glass knifefish tolerates a pH range between 3.5 and 8.4!

Behavior

Knifefishes are nocturnal, hiding during daytime between plants, in floating meadows, in crevices and holes, and under various kinds of shelter. During the day some species, such as *Rhamphichthys rostratus* and *Steatogenys elegans*, lie flat and motionless on the bottom, imitating marbled leaves. Species of the genus *Gymnorhamphichthys* burrow in the sand during daytime.

Gymnotiforms move by undulating the elongate anal fin that extends along most of the ventral part of the body. In as-

sociation with this form of locomotion, the anal fin rays articulate directly with proximal pterygophores, providing the fin rays unrestricted mobility. The caudal, elongate portion of the body is maintained in a rigid posture by numerous intermuscular bones. This facilitates the use of the integument as a sensory sheet due to the presence of numerous electroreceptors. This mechanism is used for object location. The presence of an individual nearby with an electric organ discharge frequency of similar magnitude disturbs the object location performance of the fish: a shift in frequency occurs, which is termed the jamming avoidance response.

A glass knifefish (*Eigenmannia lineata*) from the Amazon River in Brazil. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

The food of knifefishes is of indigenous origin, mostly insect larvae, annelid worms, and crustaceans. The banded knifefish predominantly feeds on shrimp and smaller fishes, as do some larger knifefishes. Electric eels are also piscivorous and include their own weakly electric relatives in their diet. Regardless of seasonal changes, *Rhamphichthys marmoratus* does not change its diet, which consists mostly of chironomids (Diptera) and polymitarcids (Ephemeroptera).

Ontogenetic change in the diet is documented for the banded knifefish: up to 7.9 in (20 cm) the principal food items are aquatic insects, predominantly chironomid larvae; beyond 7.9 in (20 cm) the fish prefer large insect larvae (Odonates), shrimp, and fish, preferably small characids (genera *Ctenobrycon* and *Curimata*). This change in diet coincides with the time when the banded knifefish females reach first maturity (9.8 in/25 cm, 2 years old).

Species of the genus *Rhabdolichops* possess well-developed gill rakers and are known to be effective plankton feeders. The knifefish *Oedemognathus exodon* feeds on scales of fishes. The knifefish *Magosternarchus duccis*, from the murky channel of the Amazon, chiefly eats the tails of other knifefishes (these do regenerate afterward).

The importance of gymnotiforms as part of the food chain is demonstrated in the case of top predators of the pimelodid family, the catfishes; fifteen commercially important pimelodid species of the Rio Apure in Venezuela include gymnotiforms in their diet. Most pimelodids feed on only one or two species; however, some pimelodids, such as *Brachyplatystoma rousseauxii*, feed on a maximum of five species.

Reproductive biology

Reproduction in most species occurs during the high-water season. Experimental studies have shown that gonad maturation is triggered mainly by decreasing water conductivity and increasing water level. Information on reproductive biology has been gathered from a limited number of species (8-9), but has consistently revealed diverse reproductive strategies. The electric eel breeds during the dry season in small ponds. The male builds a foam nest at the water surface between the adventitious roots of the plant *Montrichardia arborescens*. The eggs are deposited in the foam nest, and at the beginning of exogenous feeding, the larvae feed on eggs of subsequent ovipositions. Juveniles are guarded up to a length of 3.9 in (10 cm). The males of the banded knifefish are mouth breeders and guard the fry afterward. The longtail knifefish (*Sternopygus macrurus*) is a substrate spawner and guards the eggs until hatching. Other knifefishes hide the eggs in plants, in between roots, or in crevices. All species are fractional spawners, with spawning intervals of a few days up to several weeks. Egg diameter varies between 0.08 and 0.1 in (0.2 cm and 0.3 cm). Some species live in pairs during reproduction; others form complicated social hierarchies that are based on size, motor components of aggressive behavior, and seasonal conditions. Best studied in this respect is the glass knifefish (*Eigenmannia lineata*).

During courtship behavior, the electrical discharges serve various purposes: males and females often produce different electrical discharge frequencies, and frequency modulations of the male discharge can trigger oviposition. Large amplitudes characterize dominant males, differences in the form of the discharge occur between males and females.

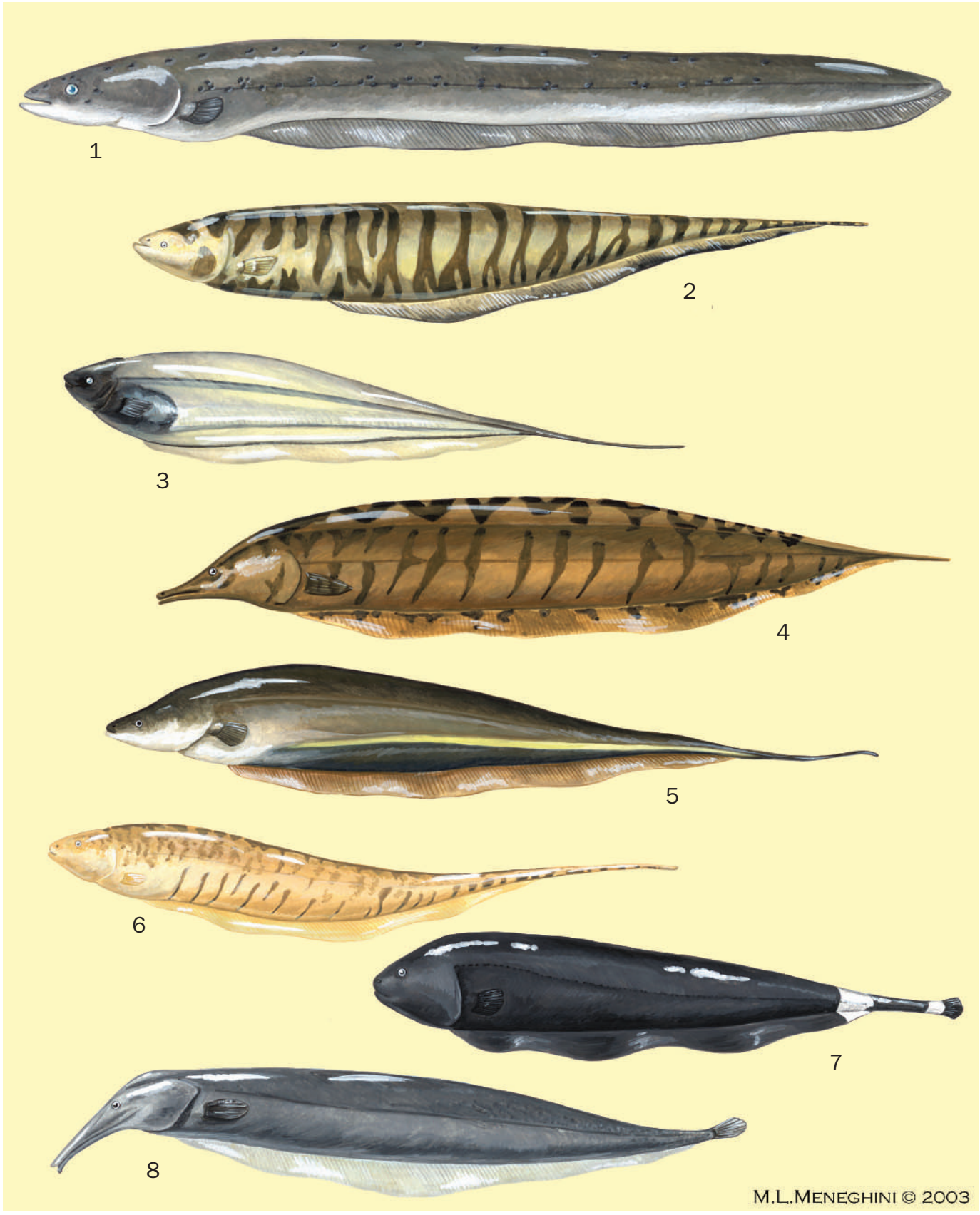
During the breeding season the males of the Rosen knifefish (*Sternarchorhynchus roseni*) develop external teeth; these knifefishes are very territorial and rather aggressive. The males of gymnotiforms often grow larger than the females. Males of several species of the genus *Apteronotus* develop longer heads than the females.

Conservation status

No gymnotiform species are listed by the IUCN.

Significance to humans

The strongly electric *Electrophorus electricus* was for decades a preferred animal for the study of basic bioelectric phenomena. The physiology, anatomy, and behavior of weakly electric knifefishes have been studied intensively, particularly in the context of orientation (object location) and electrocommunication. Some larger knifefishes, such as *Rhamphichthys rostratus* and the longtail knifefish are locally of some economical importance in fisheries.



1. Electric eel (*Electrophorus electricus*); 2. Banded knifefish (*Gymnotus carapo*); 3. Glass knifefish (*Eigenmannia lineata*); 4. Bandfish (*Rhamphichthys rostratus*); 5. Longtail knifefish (*Sternopygus macrurus*); 6. *Brachyhypopomus pinnicaudatus*; 7. Black ghost (*Apteronotus albifrons*); 8. *Sternarchorhynchus curvirostris*. (Illustration by Michelle Meneghini)

Species accounts

Black ghost
Apteronotus albifrons

FAMILY
Apteronotidae

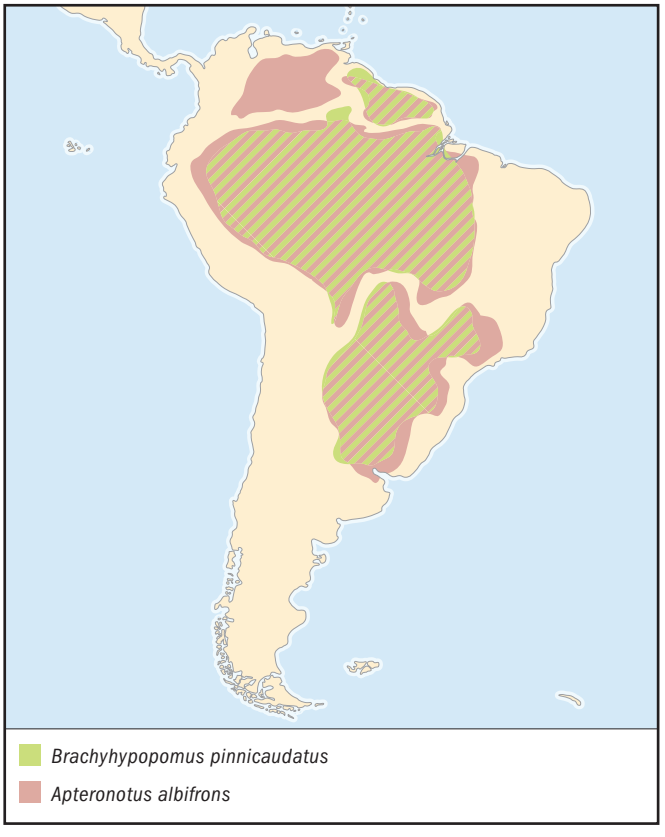
TAXONOMY
Apteronotus albifrons Linnaeus, 1766, South America.

OTHER COMMON NAMES
English: Apteronotid eel; French: Poisson-couteau; German: Amerikanischer Weißstirnmesserfisch.

PHYSICAL CHARACTERISTICS
Size 11.8 to 19.7 in (30 to 50 cm). They are completely black, except for a yellow frontal longitudinal stripe and two whitish transversal bands at the end of the anal fin and just before the black caudal fin. The males have longer heads than the females. The species is weakly electric.

DISTRIBUTION
Amazon, Orinoco, Parana-Paraguay river systems; rivers in French Guiana.

HABITAT
Occurs near undercut banks and in wooden debris along river and stream margins, as well as in densely vegetated habitats.



BEHAVIOR
Gregarious and nocturnal. During swimming movements they are not always in an upright position, often turning their body parallel to the ground.

FEEDING ECOLOGY AND DIET
Various kinds of aquatic insect larvae, as well as ants and termites. The larger fishes also eat shrimps and fishes.

REPRODUCTIVE BIOLOGY
Breeding groups of black ghosts are composed of several males and females. As oviposition does not occur in regular intervals, single eggs of 0.1 in (0.3 cm) are deposited in holes and crevices, rather irregularly. The embryos hatch on day three, feeding starts on day 10.

CONSERVATION STATUS
Not listed by the IUCN

SIGNIFICANCE TO HUMANS
Black ghosts are the most common knifefishes in the tropical-fish trade. They are regarded by indigenous people with superstition, as they are reputed to be inhabited by a ghost or an evil spirit. ◆

No common name
Sternarchorhynchus curvirostris

FAMILY
Apteronotidae

TAXONOMY
Sternarchorhynchus curvirostris Boulenger, 1887, Canelos, Ecuador.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Size from 15.7 to 19.7 in (40 to 50 cm). Their bodies are extremely compressed, with a pronounced curved snout; they lack dorsal and pelvic fins. The skin is uniformly brown. The electric organ is weak as it is derived from nerve cells (neurogenic) as opposed to muscle tissue (myogenic).

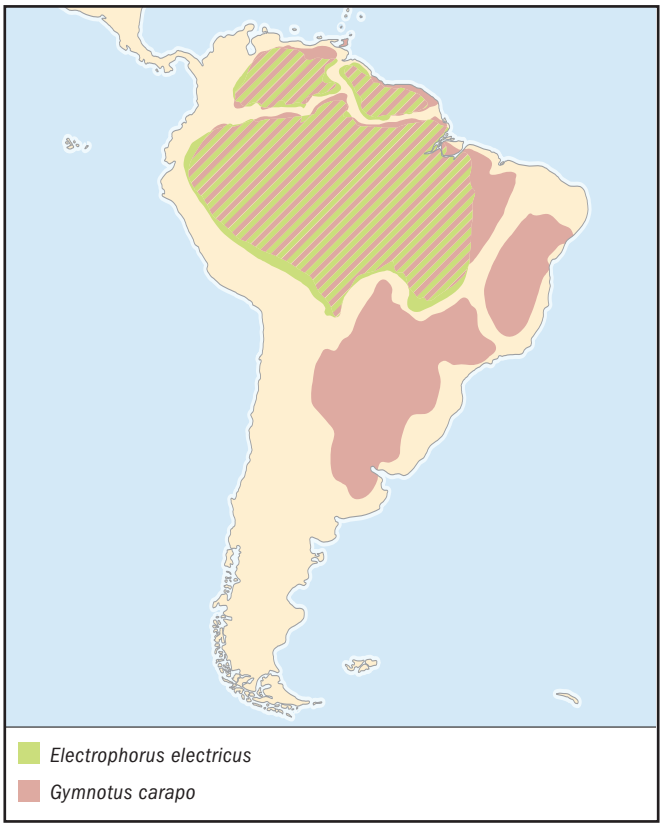
DISTRIBUTION
Amazon and Orinoco river systems; rivers in the Guyanas.

HABITAT
Channel bottom of large rivers.

BEHAVIOR
Nocturnal, feeding (and probably spawning) at night. Territorial and rather aggressive.

FEEDING ECOLOGY AND DIET
Insect larvae and possibly smaller crustaceans.

REPRODUCTIVE BIOLOGY
Probably spawn during the rainy season. Other details of their reproductive biology are not known.



CONSERVATION STATUS
Not listed by IUCN. They are common throughout their range of distribution but at low densities.

SIGNIFICANCE TO HUMANS
None known. ◆

Electric eel
Electrophorus electricus

FAMILY
Gymnotidae

TAXONOMY
Electrophorus electricus Linnaeus, 1766, South America.

OTHER COMMON NAMES
French: Anguille électrique; anguille trembleuse; German: Zitteraal; Spanish: Anguilla, anguilla electrica; Portuguese: Poraquê.

PHYSICAL CHARACTERISTICS
Electric eels are the largest of all knifefishes, up to 8 ft (2.4 m) long. They lack dorsal, caudal, and pelvic fins, and do not have scales. The color is a uniform dull olive to almost black, yellowish to orange underneath the head and throat. These fishes produce strong electric discharges up to 700 volts.

DISTRIBUTION
Rivers in the Guyanas; the Amazon and Orinoco river systems.

HABITAT
Occurs in creeks and ponds, and along the banks of lakes.

BEHAVIOR
Nocturnal. They hide during the day under shelter or in holes. They are sometimes gregarious.

FEEDING ECOLOGY AND DIET
These fishes are mostly piscivorous (they stun prey with electric shocks), but they also eat amphibians.

REPRODUCTIVE BIOLOGY
These fishes breed during the dry season in small ponds. The male builds a foam nest. The larvae first eat eggs of subsequent spawnings, then change diet to insect larvae. Piscivorous feeding starts at around 3.9 in (10 cm); the males guard juveniles up to this size.

CONSERVATION STATUS
Not listed by the IUCN. They are common throughout their range of distribution but at low densities.

SIGNIFICANCE TO HUMANS
Electric eels have been used for basic studies on bioelectric phenomena. ◆

Banded knifefish
Gymnotus carapo

FAMILY
Gymnotidae

TAXONOMY
Gymnotus carapo Linnaeus, 1758, South America.

OTHER COMMON NAMES
English: Eel knifefish; gymnotid eel; cutlass fish; French: Coutelas; German: Gebänderter Messerfisch.

PHYSICAL CHARACTERISTICS
Banded knifefishes range in size from 19.7 to 23.6 in (50 to 60 cm). They have an eel-like body shape, with a blunt head, and extend to a fine point at the tip of the tail. The anal fin originates close behind the anus and continues to the tip of the tail. These fishes are variable in color, with many dark bands, and are sometimes mottled. The bands become increasingly narrow toward the tail. Banded knifefishes are air-breathing (with swim bladder), and are weakly electric.

DISTRIBUTION
Tropical South America from Venezuela to Uruguay, including Trinidad.

HABITAT
Creeks and ponds and along the banks of lakes and rivers.

BEHAVIOR
Nocturnal, hiding during daytime under various types of shelter. They are territorial, defending areas of several square yards (meters).

FEEDING ECOLOGY AND DIET
Banded knifefishes up to 7.9 in (20 cm) long eat insect larvae; afterwards odonats (dragonflies), shrimps, and fish.

REPRODUCTIVE BIOLOGY
Banded knifefishes spawn during the rainy season. Sticky eggs are deposited in between the stalks of plants. Males build nests from plant material and guard the free embryos in their mouths until the start of exogenous feeding. The first reproduction in captivity was in 1999.

CONSERVATION STATUS
Not listed by the IUCN. They are widespread and common but at low densities.

SIGNIFICANCE TO HUMANS
These weakly electric fishes are studied regularly for scientific purposes. They are extensively fished for and eaten in their native range. ◆

No common name

Brachyhypopomus pinnicaudatus

FAMILY
Hypopomidae

TAXONOMY
Brachyhypopomus pinnicaudatus Hopkins 1991 coastal swamp in French Guiana, 3.5 km northwest of Kourou.

OTHER COMMON NAMES
French: Poisson-couteau; Creole/French: Poson-sab, bloblo; Portuguese: Tuvira, itui.

PHYSICAL CHARACTERISTICS
These fishes range in size from 4.7 to 5.9 in (12 to 15 cm). Their bodies are compressed laterally; they lack dorsal, tail, and pelvic fins. Their bodies have a light-brown or reddish background with 22–25 narrow, dark brown bands running from the base of the anal fin dorsally to the lateral line. The dorsal surface is dark brown and reticulated, with distinct contrasting borders. The tail filament is compressed in males, pointed in females. These fishes are weakly electric.

DISTRIBUTION
Rivers in French Guiana and southeastern Brazil; Amazon and Parana-Paraguay river systems.

HABITAT
Occurs along the edges of slow-moving rivers and in standing water, often in dense vegetation that becomes stagnant and partially deoxygenated.

BEHAVIOR
Nocturnal, resting during the day in dense vegetation.

FEEDING ECOLOGY AND DIET
Aquatic insects and copepods (small crustaceans).

REPRODUCTIVE BIOLOGY
Reproduction in these fishes occurs mainly during the high-water season; some populations seem to show aperiodical reproduction. Sticky eggs are deposited in crevices and holes, and in between plants. The embryos hatch on day three, exogenous feeding starts on day eight to nine; the juveniles grow quickly.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Bandfish

Rhamphichthys rostratus

FAMILY
Rhamphichtyidae

TAXONOMY
Rhamphichthys rostratus Linnaeus, 1766, South America.

OTHER COMMON NAMES
Spanish: Bombilla (Argentina), cuchillo (Venezuela); French Guiana: Wabri.

PHYSICAL CHARACTERISTICS
Bandfishes range in size from 3.3 to 4.9 ft (1 to1.5 m). This most striking knifefish has a long, trunklike snout, ending in a small mouth. Otherwise, the body form is as in most knifefishes. Bandfishes lack dorsal, tail, and pelvic fins. They are medium brown in color, with blotches of dark brown and black on the back, and brown mottling on the sides. They are weakly electric.

DISTRIBUTION
Amazon, Parana-Paraguay, and Orinoco river systems; rivers of Guyana and northeastern Brazil.

HABITAT
Small and more open streams, and occasionally in large rivers.

BEHAVIOR
Nocturnal. During the day they hide motionless in plants or on the bottom.

FEEDING ECOLOGY AND DIET
Bandfishes are bottom feeders; they eat oligochaets (annelid worms) and insect larvae.

REPRODUCTIVE BIOLOGY
Bandfishes spawn during the rainy season. Data on reproduction in captivity known from one *Rhamphichtys* species, probably *R. rostratus.* About 1,000 sticky eggs are deposited in crevices; the embryos have attachment organs. Spawning intervals between three and four weeks. Juveniles show quick growth.

CONSERVATION STATUS
Not listed by the IUCN. They are widespread and common but at low densities.

SIGNIFICANCE TO HUMANS
Bandfishes are highly regarded as a food fish in areas where they are common. ◆

Glass knifefish
Eigenmannia lineata

FAMILY
Sternopygidae

TAXONOMY
Eigenmannia lineata Müller and Troschel, 1849, Lake Amucu, French Guiana.

OTHER COMMON NAMES
English: Green knifefish; German: Grüner Messerfisch; Spanish: Chucho, ratón, mayupa; Portuguese: Tuvira.

PHYSICAL CHARACTERISTICS
Female glass knifefishes are 7.9 (20 cm) long; males are 13.8 in (35 cm). Their bodies are slender and compressed, possessing only pectoral fins and the very long anal fin. Most of the fish is very transparent, except in the head region. There are three black stripes running lengthwise along the body. Glass knifefishes are weakly electric.

DISTRIBUTION
Amazon, Orinoco, and Parana-Paraguay river systems.

HABITAT
Occurs near undercut banks and in wooden debris along river and stream margins; in the open-water areas of small creeks, lagoons, and marshes; and particularly in densely vegetated habitats of river margins.

BEHAVIOR
Gregarious and nocturnal. During daytime can be sometimes found in large numbers in hiding places.

FEEDING ECOLOGY AND DIET
Aquatic insect larvae and crustaceans.

REPRODUCTIVE BIOLOGY
Glass knifefishes spawn during rainy season; breeding groups of several fish establish complicated social hierarchies. The dominant male spawns with the ripe female at night. Sticky eggs are deposited on floating plants; they hatch on day three. Exogenous feeding begins on day eight.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Glass knifefishes are the most intensively studied species of knifefish. They are often designated as *Eigenmannia virescens.* The systematics of the genus *Eigenmannia* is very difficult, which often leads to misidentification. The fish sold in the fish trade is in general called *E. virescens* (this name therefore often appears in scientific papers); however, the morphological features of this fish make it clear that it is not *E. virescens* but rather *E. lineata*. ◆

Longtail knifefish
Sternopygus macrurus

FAMILY
Sternopygidae

TAXONOMY
Sternopygus macrurus Bloch and Schneider, 1801, Brazil.

OTHER COMMON NAMES
English: Ghost knifefish; Spanish: Bio del rio.

PHYSICAL CHARACTERISTICS
Longtail knifefishes range in size from 23.6 to 31.5 in (60 to 80 cm), and are among the largest knifefishes. They have a pale yellow skin, a large black humeral spot; and a pale-yellow or white longitudinal stripe along the base of the anal fin, pterygiophores, and lateral midline posteriorly. They are weakly electric.

DISTRIBUTION
Amazon, Orinoco, and Parana-Paraguay river systems; rivers of northeastern and southeastern Brazil.

HABITAT
Widely distributed in streams, trenches, ditches, and the back waters of rivers in open savanna and in plantations.

BEHAVIOR
Mainly active at dusk and dawn, when the light level is low; they forage at night. They are territorial, slow-moving fishes.

FEEDING ECOLOGY AND DIET
When young, longtail knifefishes feed on small crustaceans and insect larvae. During growth, their diet changes to larger organisms such as shrimps and fishes. Adult insects are an important food item at all stages.

REPRODUCTIVE BIOLOGY
Longtail knifefishes mature when they are 11.8–15.7 in (30–40 cm) long. Several hundred 0.1 in (0.3 cm) eggs are deposited on a substrate. The male guards the eggs, which hatch after three days. The larval stage begins at 10 days.

CONSERVATION STATUS
Not listed by the IUCN. They are common throughout their range of distribution but at low densities.

SIGNIFICANCE TO HUMANS
Longtail knifefishes are fished for and eaten in their native range. The flesh is firm and considered to have a good flavor. ◆

Resources

Books

Albert, J. *Species Diversity and Phylogenetic Systematics of American Knifefishes (Gymnotiformes, Teleostei).* Ann Arbor: Museum of Zoology (University of Michigan), 2001.

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Kirschbaum, F., and L. Wieczorek. *Entdeckung einer neuen Fortpflanzungsstrategie bei südamerikanischen Messerfischen (Teleostei: Gymnotiformes: Gymnotidae): Maulbrüten bei Gymnotus carapo.* Vol. 2. In *Verhalten der Aquarienfische*, edited by H. Greven and R. Riehl. Bornheim, Germany: Birgit Schmettkamp Verl., 2002.

Mago-Leccia, F. *Electric Fishes of the Continental Waters of America.* Vol. 29, *Biblioteca de la Academica de Ciencias Fisicas Matematicas y Naturales.* Caracas, Venezuela: FUDECI, 1994.

Moller, P., ed. *Electrical Fishes: History and Behavior. Fish and Fisheries Series 117.* London: Chapman & Hall, 1995.

Periodicals

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Frank Kirschbaum, PhD

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Esociformes

(Pikes and mudminnows)

Class Actinopterygii

Order Esociformes

Number of families 1 or 2

Photo: A central mudminnow (*Umbra limi*) burrows into the mud to escape predators. (Photo by Gregory K. Scott/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Three key questions to consider regarding the evolution of esociforms are: When did they originate? What other group of fishes is their closest relative? And, what are the evolutionary relationships among esociform species?

As of 2002, the earliest evidence of esociform fishes in the fossil record was in the form of fragmentary fossils found in deposits dating to the Upper Cretaceous from Alberta, Canada. The evidence consists of numerous fossilized fragments of bones that form the mouth skeleton, which displays a distinctive form of tooth attachment that is characteristic of living esociform species. Almost complete fossils of esociform fishes are found in Paleocene deposits from Alberta and Eocene deposits from Wyoming, United States. These fossils are extremely similar to living species of *Esox*. The fossil evidence suggests that esociform fishes belong to an ancient fish lineage that is more than 70 million years old.

Unfortunately, scientists have a poor understanding of the relationship of esociforms to other fish groups of similar age. The many primitive anatomical features that characterize esociforms hinder the development of a satisfactory theory on the classification of esociforms, despite a long history of phylogenetic studies on this area of fish evolution. Systematic studies based on anatomical comparisons have yielded tentative conclusions based on scant evidence. Studies based on comparisons of genetic sequences have produced the most strongly supported hypothesis of esociform relationships. These studies show unequivocal support for a close evolutionary relationship between the fishes in the order Salmoniformes (i.e., salmons, trouts, chars) and the esociforms. However, a consensus hypothesis is not available.

The order Esociformes includes four genera and 10 to 12 species, depending on the validity of two species described in 1982 from Siberia. The four genera of Esociformes are:

- *Dallia* (Alaska blackfish or dogfish)
- *Esox* (Northern pike, muskellunge, and pickerels)
- *Novumbra* (Olympic mudminnow)
- *Umbra* (European, central, and eastern mudminnows)

Until the late 1990s, esociform genera were divided into two families: Esocidae, for the genus *Esox*; and Umbridae, for the remaining three genera, which are collectively termed the mudminnows. This classification conflicts with molecular data first reported in 2000, which showed that these two families do not represent natural evolutionary groups. The molecular evidence suggests that the genera *Esox* and *Novumbra* are the closest evolutionary relatives, and that *Umbra* is the most primitive of the four esociform genera. In light of this evidence, the traditional two-family division of esociforms should be disregarded. A one-family scheme is followed in this chapter but, as of 2002, there was no general agreement on the classification of esociform genera.

Physical characteristics

One striking characteristic of all living esociforms is the posterior placement of the dorsal fin, which is located nearly opposite the anal fin in all species. Esociforms have elongate bodies with round cross sections. *Esox* species are further characterized by a flattened and elongated snout, which somewhat resembles a duck's bill.

Most species are small or medium sized; but *Esox* includes very significant exceptions. For example, individuals of *E. masquinongy* may reach over 5 ft (1.6 m) in length and weigh more than 66 lb (30 kg). At the other end of the scale, individuals of the four species in *Novumbra* and *Umbra* rarely reach 4 in (10 cm) and weigh less than 1 oz (28.3 g). In light of their marked contrast in size, it is interesting to note that *Esox* and *Novumbra* are thought to be very close relatives.

The coloration of esociforms is varied, but markings or mottled patterns on brown or olive green backgrounds are a common feature. A mottled coloration pattern in the densely vegetated habitats that esociforms favor likely hinders their detection by prey and/or predators. Males of some species show intensified coloration during the breeding season, with attractive iridescent hues on the body and fins.

Distribution

Living species of esociforms are found in all major Northern Hemisphere landmasses, with the exception of Greenland. North America is home to eight species of esociforms, three are found in northern Asia, and two inhabit European waters. The fossil record shows that the diversity of species of esociforms in Europe and Asia has been higher in the past. However, as of 2002, there was no evidence to indicate major changes in the global distribution of the order over its evolutionary history.

There have been changes in the distribution of some esociform species due to human intervention. The ranges of species in *Novumbra* and *Umbra* have undergone attrition due to habitat destruction. In contrast, the natural distributions of some *Esox* species have been expanded by human intervention because of their value as sport fishes.

Habitat

The understanding of the biology of esociforms is much more extensive for members of the genus *Esox* because these species are important in recreational fishing. However, the few studies conducted on the biology of the other esociform species point to broad similarities among all members of the order. Adults of the larger species of *Esox* move freely between shore and open water habitat. All esociforms show a similar preference for still or slow-moving water where dense vegetation allows them a place to hide. Other than dense vegetation, mudminnows seek areas with thick and loose muddy substrate, into which they quickly dive when startled. In addition, mudminnows have modified areas of the gut and swim bladder to extract oxygen from ingested atmospheric air. This allows them to withstand the widely fluctuating oxygen levels that may be associated with the heavy vegetation and rich organic matter substrate characteristic of their habitat.

Behavior

Outside the breeding season, esociforms are solitary and sedentary. They are most often found hovering among vegetation using elegant and economical pectoral and medial-fin movements to remain in place, with occasional pelvic-fin motions to correct body orientation. From this stance, the pikes wait for their prey, which they capture with a fast strike. Mudminnows may perch on the vegetation or rest on the substrate, eliminating the need for any fin movement. When dissolved oxygen levels are low, mudminnows occasionally swim up to the water surface and gulp air.

Feeding ecology and diet

Esociformes are carnivorous, predatory fishes. All *Esox* species prey most commonly on fishes, including smaller individuals of their own species. The larger species may also prey on frogs, waterfowl, and small mammals; their diets seem to be limited only by the size of the potential prey item and the opportunity for its capture. The mudminnows and the Alaska blackfish are also carnivorous, but due to their small size their diet consists almost entirely of aquatic invertebrates and, very rarely, juvenile fish.

Adult northern pike and muskellunge have only a few opportunistic natural predators, including bears, otters, and large birds of prey. Juveniles and fry of species of *Esox* are commonly preyed upon by larger members of the genus and other predatory fishes that share their habitat (e.g., centrarchid basses). The blackfish and the Olympic mudminnow have few predators because they occupy areas with few other species and are often found among thick vegetation that prevents terrestrial predators from targeting them. Pikes, pickerels, and other piscivorous fishes prey on mudminnows of the genus *Umbra*.

Reproductive biology

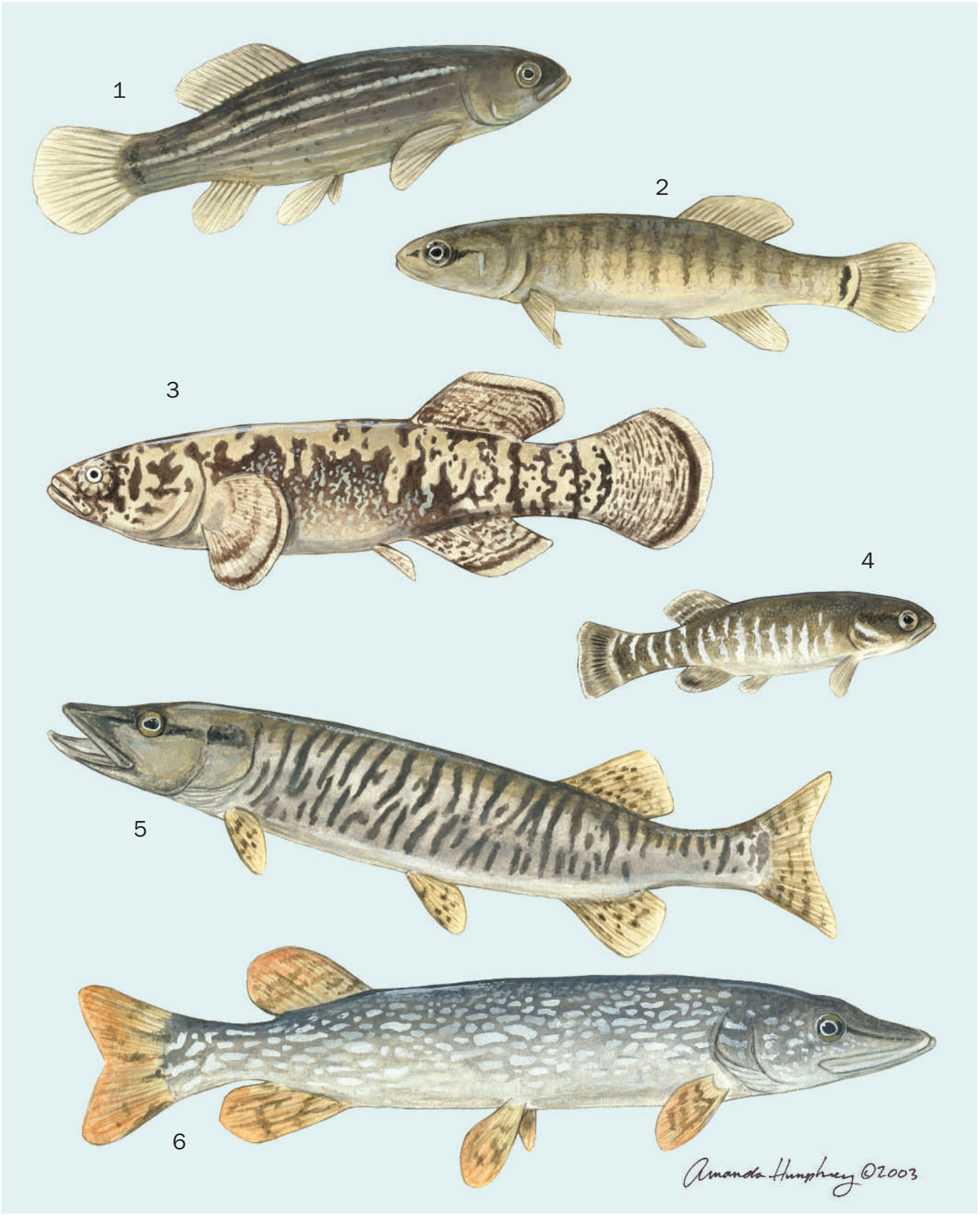
Most esociforms spawn early in the spring when water temperatures begin to rise. Some populations must undertake a migration to reach the spawning grounds. There is no evidence of nest building, but there are reports of territoriality around the spawning site in species of *Novumbra* and *Umbra*. Spawning most often involves one female and a few to several males. In some species, the males court the females through swimming displays or aggression. Egg deposition is usually preceded by exaggerated swimming motions and side-to-side contact. Eggs may stick to vegetation or drop to the ground. Fry do not receive parental care.

Conservation status

Habitat destruction is the main threat to populations of esociforms. Mudminnows are particularly vulnerable to this threat because they occur in areas with large human populations, and their habitat preference is not compatible with traditional land-development practices. The European mudminnow (*Umbra krameri*) is classified as Vulnerable by the IUCN, while the Olympic mudminnow (*Novumbra hubbsi*) is classified as Lower Risk/Near Threatened. Due to the interest of recreational anglers on all species of *Esox*, management policies and fishing regulations are in place to ensure stable populations.

Significance to humans

The greatest interest of humans in these fishes in modern times is limited to those species, all of which are members of the genus *Esox*, targeted by recreational anglers. There has been sporadic interest by aquarium enthusiasts in various mudminnows. Historically, some human populations indigenous to Siberia and Alaska have included blackfish in their diet.



1. European mudminnow (*Umbra krameri*); 2. Central mudminnow (*Umbra limi*); 3. Alaska blackfish (*Dallia pectoralis*); 4. Olympic mudminnow (*Novumbra hubbsi*); 5. Muskellunge (*Esox masquinongy*); 6. Northern pike (*Esox lucius*). (Illustration by Amanda Humphrey)

Species accounts

Alaska blackfish
Dallia pectoralis

FAMILY
Esocidae

TAXONOMY
Dallia pectoralis Bean, 1880, Saint Michaels, Alaska, United States.

OTHER COMMON NAMES
English: Dogfish; French: Dallia; German: Fächerfisch; Russian: Chernaya ryba.

PHYSICAL CHARACTERISTICS
Length 1.9–6.3 in (4.8–16 cm); specimens as large as 13 in (33 cm) have been recorded; males reach larger sizes due to their longer lifespan. Stout head, well-developed fanlike pectoral fins, and much-reduced pelvic fins. Usually with a brown mottled pattern on a light cream background and light margins on the fins.

DISTRIBUTION
Lowlands of northern and western Alaska and the Chukot Peninsula of eastern Siberia. Introduced and established in Anchorage and St. Paul Island. Populations of *Dallia* that inhabit Arctic drainages of eastern Siberia may represent two different species of this genus.

HABITAT
In the spring and summer, occurs in shallow ditches and lakeshores with little or no water movement and thick vegetation. In winter, may move to deeper areas to avoid freezing.

BEHAVIOR
Mostly unknown. Their ability to tolerate extremely low temperatures is well known but not thoroughly understood; behavioral and/or physiological adaptations are probably involved. A gas-exchange organ associated with the esophagus allows them to obtain oxygen from gulped air, thus allowing them to occupy waters with low concentration of dissolved oxygen.

FEEDING ECOLOGY AND DIET
Preys predominantly on crustaceans (caldocerans, copepods, and ostracods) and aquatic insect larvae. Other aquatic invertebrates and, rarely, fish complement the diet.

REPRODUCTIVE BIOLOGY
The timing of spawning varies, depending on seasonal conditions at a given location. A population near Fairbanks, Alaska, spawns during May and June. Some populations undertake a migration to the spawning grounds in spring when thawing makes these areas available. Mature females carry 40–300 sticky, transparent eggs. Little is known about spawning behavior.

CONSERVATION STATUS
Not threatened. Widespread and abundant in their native range. Their remote distribution protects their habitat from destruction by human action. As of 2002 in the United States, it was illegal to transport live blackfish out of their native range without a permit.

SIGNIFICANCE TO HUMANS
Some indigenous communities have relied heavily on blackfish for food for themselves and their dogs. The nutritive value of blackfish was greatest in the winter when other sources of protein were scarce and these communities faced starvation. In modern times human consumption of blackfish has decreased, probably as a result of year-round availability of other foods. ◆

Northern pike
Esox lucius

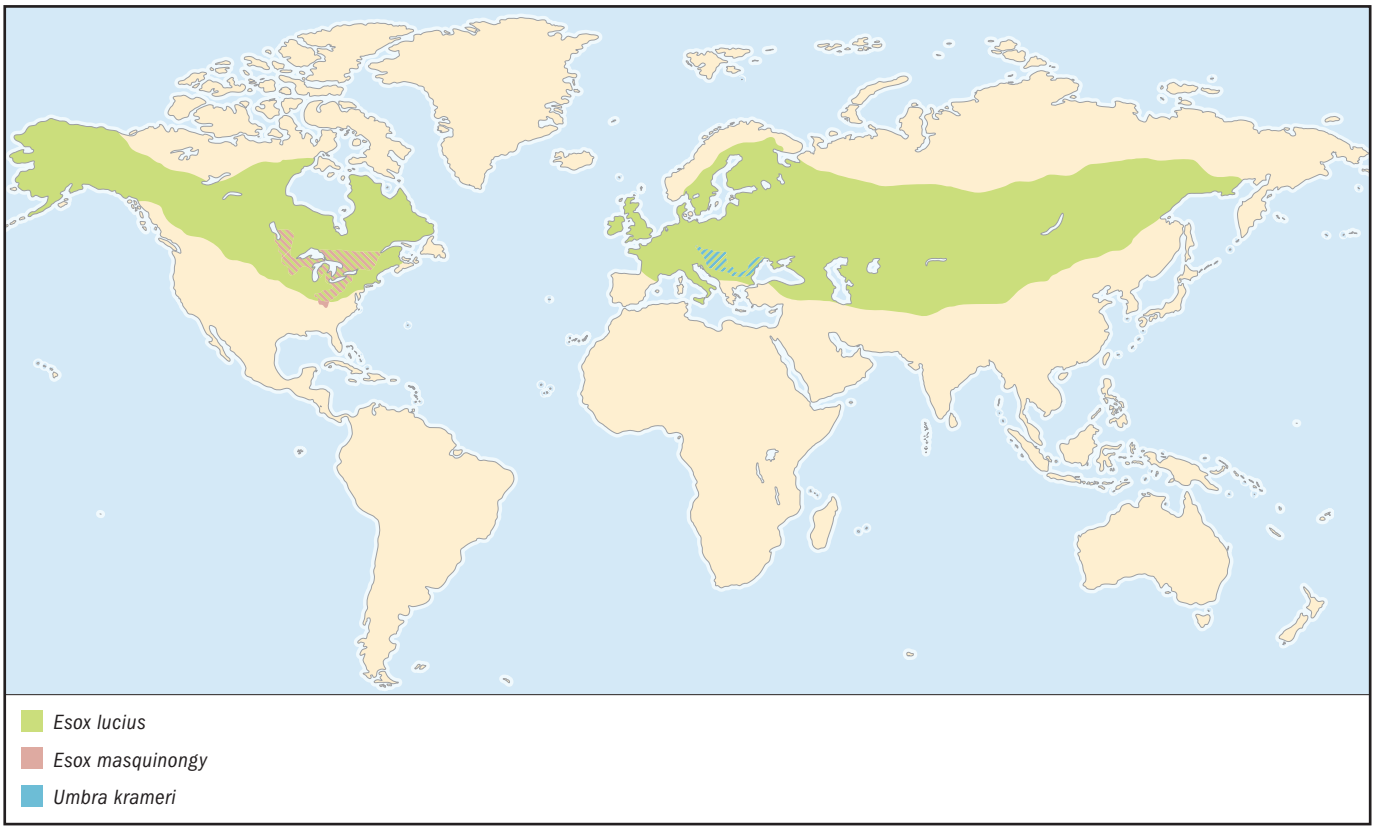
FAMILY
Esocidae

TAXONOMY
Esox lucius Linnaeus, 1758, Europe.

OTHER COMMON NAMES
English: Jack, luce; French: Brochet; German: Hecht; Russian: Shchuka; Spanish: Lucio.

PHYSICAL CHARACTERISTICS
Standard length 35.4 in (90 cm); standard weight 24.2 lb (11 kg); flattened, elongate snout, scales on cheek and operculum. Long, cylindrical body with irregular yellow spots on a silvery green background that is lighter towards the belly. Stoutness of body varies depending on growing conditions, with better conditions resulting in deeper-bodied fish.

DISTRIBUTION
Northern North America, Europe, and Asia. Introduced by humans to Africa, Ireland, and Spain.



HABITAT
Prefers cool lakes, ponds, and slow-moving rivers with abundant vegetation. Young and smaller adults occupy shallow shore areas and move to greater depths as they grow.

BEHAVIOR
Solitary outside the breeding season. Hovers almost motionless among vegetation in wait for unsuspecting prey. May remain in same location for long periods of time if food is plentiful, otherwise will range over large distances in habitat with low prey density.

FEEDING ECOLOGY AND DIET
Voracious sit-and-wait predator; feeds on any animal large enough to be worth the effort and small enough to be subdued. Fish are the largest component of the diet. Fry feed on invertebrates until they are able to take fish. Fry and juveniles fall prey to larger individuals of the species, as well as to frogs and large aquatic insects. Adults are vulnerable to osprey and other large fish-eating birds, as well as otters, bears, and commercial and recreational fishing.

REPRODUCTIVE BIOLOGY
Spawning occurs in early spring. Males and females move close to shore or from streams to marshy areas. One female and a few smaller males swim into shallow vegetated areas. Females release a small number of eggs, which are immediately fertilized by attendant males. Egg release is repeated a varying number of times. Females may carry as many as 250,000 eggs. Both males and females may spawn with different mates during a spawning season. Adults do not guard spawning sites or provide care to the young.

CONSERVATION STATUS
Not threatened. Many populations are managed to maintain strong recreational fishing. Habitat destruction is a threat in some parts of their distribution, but worldwide they are not at risk.

SIGNIFICANCE TO HUMANS
In modern times, they are highly valued sport fishes and the focus of a recreational fishery of substantial economic importance. In the past, they were also valued as food fishes, and a sizable commercial fishery existed. Some praise the flavor of their flesh, but demand is not widespread and the commercial fishery is small. ◆

Muskellunge
Esox masquinongy

FAMILY
Esocidae

TAXONOMY
Esox masquinongy Mitchill, 1824, Lake Erie, North America.

OTHER COMMON NAMES
English: Lunge, muskie, mascalonge.

PHYSICAL CHARACTERISTICS
Standard weight 33 lb (15 kg); scales only on upper half of cheek and operculum. Prominent sensory pores on lower jaw. Dark spots or mottled markings on a silver or light green body, but color variation exists between populations in different parts of their distribution and markings may be absent.

DISTRIBUTION
Northeastern North America; centered around Great Lakes region.

HABITAT
As with *E. lucius*, prefers slow-moving or still waters with abundant vegetation, but with slightly warmer water temperatures.

BEHAVIOR
Mostly sedentary among vegetation. Hovers among aquatic vegetation, striking at prey with a fast, powerful lunge. For unknown reason, sometimes floats just beneath the water surface with the back exposed to the air.

FEEDING ECOLOGY AND DIET
Voracious predators; predominantly feed on fishes, but are known to eat crayfishes, frogs, waterfowl, and small mammals. Fry begin eating small invertebrates until they are able to capture larger prey. Fry are often eaten by *E. lucius* fry, which hatch some weeks earlier. Subadults are vulnerable to ospreys and other large fish-eating birds, as well as otters, bears, and commercial and recreational fishing. Large adults have no predators other than humans.

REPRODUCTIVE BIOLOGY
Spawns in spring when water temperature reaches 49–59°F (9.4–15°C). Similar courtship and spawning behavior as *E. lucius*, but avoids areas where that species spawns by releasing eggs in deeper water. In nature, these two species form sterile hybrids that are known as tiger muskies.

CONSERVATION STATUS
Not threatened. However, this species is rare in some areas and these populations are protected. Recreational fishing is strictly managed.

SIGNIFICANCE TO HUMANS
Numerous businesses profit from activities related to recreational angling in Canada and the United States. Winter fishing for these and other fishes through the ice using spears is a valued part of the cultural tradition of some Native American communities, and is still practiced in part of Wisconsin. ◆

Olympic mudminnow
Novumbra hubbsi

FAMILY
Esocidae

TAXONOMY
Novumbra hubbsi Schultz, 1929, near Satsop, Washington, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Length 1–3.4 in (2.5–8.5 cm); light to dark brown with light green vertical stripes along the entire length of the fish. Dark vertical bar across eye. Males develop a striking breeding coloration consisting of green to blue iridescent vertical stripes on an almost black background.

DISTRIBUTION
Restricted to lowlands of south and west drainages of the Olympic Peninsula in Washington State, United States, and a few drainages of the Puget Sound. Not known whether the Puget Sound populations are native or introduced.

HABITAT
Ponds, ditches, or creeks with still or slow-moving water, abundant submerged vegetation, and, usually, a thick layer of loose mud substrate

BEHAVIOR
Can survive in water with low oxygen content and under a wide range of temperatures, but shows little tolerance for salinity.

FEEDING ECOLOGY AND DIET
Feeds on aquatic invertebrates; primarily ostracods, isopods, worms and aquatic insects. Tends to coexist with only a few other fish species; primarily the reticulate sculpin (*Cottus perplexus*) and the three-spined stickleback (*Gasterosteus aculeatus*). Reticulate sculpins may prey on juvenile mudminnows. Although vulnerable to fish-eating birds, adults appear to have few predators.

REPRODUCTIVE BIOLOGY
Peak spawning occurs in April and May, but can take place from November to June with a lull in the winter. Males defend territories and perform a courtship display for passing females. Mating pairs wiggle in place side by side and spawn repeatedly, releasing a few eggs at a time. Eggs stick to vegetation or the substrate. Fry remain in place for about one week before dispersing. Parental care has not been documented.

CONSERVATION STATUS
Listed as Lower Risk/Near Threatened by the IUCN, as habitat destruction is a significant threat due to a very restricted distribution. The state of Washington gives the species special management consideration.

SIGNIFICANCE TO HUMANS
None known. ◆

European mudminnow
Umbra krameri

FAMILY
Esocidae

TAXONOMY
Umbra krameri Walbaum, 1792, Danube River, Europe.

OTHER COMMON NAMES
German: Hundsfisch; Hungarian: Lápi póc; Russian: Evdoshka; Ukrainian: Boboshka, lezheboka.

PHYSICAL CHARACTERISTICS
Length 2–3.5 in (5–9 cm); elongated body is slightly flattened dorsoventrally. Dorsal fin has almost rectangular profile. Drab brown coloration with a light horizontal stripe through the middle of the body.

DISTRIBUTION
Lowlands of the Danube River drainage from Vienna to the Black Sea, as well as the Prut and Dniester Rivers.

HABITAT
Oxbow lakes, ditches, and ponds with dense vegetation and debris.

BEHAVIOR
Few field studies have examined behavior.

FEEDING ECOLOGY AND DIET
Feeds mainly on aquatic crustaceans and insect larvae; rarely fish fry and vegetation. Main predators are piscivorous waterfowl, predatory fishes (including young of *E. lucius*), and large insects.

REPRODUCTIVE BIOLOGY
Spawning takes place from February to April. Several males pursue ripe females, which become progressively more receptive to their attention. Females that are ready to spawn find a suitable patch of vegetation and swim into it, followed by several attentive males. Males position themselves next to the females and eggs and sperm are released. The eggs may stick to the vegetation or sink to the bottom. After an interval of varying length, the process is repeated until the female has exhausted her egg supply. The female subsequently guards her spawning territory, but does not seem to take special care of the eggs or fry.

CONSERVATION STATUS
Habitat destruction has led to extirpation from a large part of the known historical distribution. Flood control of rivers and wetland development destroy its required habitat. Pollution affects all drainages where it exists. As a result, classified as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Of no interest to commercial or recreational fisheries. In the past, used to feed livestock and as crop fertilizer. Because they represent a unique evolutionary lineage, countries where viable populations exist use this species to stimulate wildlife awareness and education. ◆

Central mudminnow
Umbra limi

FAMILY
Esocidae

TAXONOMY
Hydrargira limi Kirtland, 1840, Yellow Creek, Trumbull County, Ohio, United States.

OTHER COMMON NAMES
English: Dogfish, mudfish, mudpuppy; German: Amerikanischer Hundsfisch.

PHYSICAL CHARACTERISTICS
Length 1.6–3.9 in (4–10 cm); short cylindrical body. Dark brown to green, with lighter, irregular vertical stripes along the length of the body.

DISTRIBUTION
Centered around the Great Lakes region from northern Tennessee, United States, to southern Manitoba and Quebec, Canada.

HABITAT
Still or slow-moving water in ponds and ditches with a thick layer of mud on the bottom and abundant aquatic vegetation.

BEHAVIOR
Little information available. Sedentary in vegetation or resting on substrate, moving only to forage or to gulp air from surface. Capable of obtaining oxygen from air through the swim bladder. Evades predators by diving into the muddy substrate.

FEEDING ECOLOGY AND DIET
Carnivorous; feeds on aquatic invertebrates, particularly crustaceans and insect larvae. Important predators are juveniles of *Esox* species. Also vulnerable to water snakes and fish-eating birds.

REPRODUCTIVE BIOLOGY
Spawning takes place in the early spring on flooded banks. Mature females carry 200–2,200 eggs. Eggs are sticky and deposited in dense vegetation, where they hatch after about six days. Fry are not guarded or cared for by parents.

CONSERVATION STATUS
Not listed by IUCN. Rare in the western and southern limits of their distribution, probably as a result of habitat alteration. Widespread and abundant where their habitat is available. Habitat destruction by flood control and draining of wetlands is an ongoing threat.

SIGNIFICANCE TO HUMANS
Of no interest as a food fish. Because they are hardy, considered good for bait in some regions, but drab coloration reduces their value to the angler. Of some interest to aquarists. ◆

Resources

Books

Craig, John F., ed. *Pike Biology and Exploitation.* New York: Chapman & Hall, 1996.

Morrow, James E. "Mudminnows and Blackfish." In *The Freshwater Fishes of Alaska.* Anchorage: Alaska Northwest Publishing Co., 1980.

Scott, William B., and E. D. Crossman. "Mudminnows: Umbridae." In *Freshwater Fishes of Canada.* Oakville, Ontario: Galt House Publishing, 1998.

———. "Pikes: Esocidae." In *Freshwater Fishes of Canada.* Oakville, Ontario: Galt House Publishing, 1998.

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Grande, L. "The First *Esox* (Esocidae: Teleostei) from the Eocene Green River Formation, and a Brief Review of Esocid Fishes." *Journal of Vertebrate Paleontology* 19 (1999): 271–292.

López, J., T. Pietsch, and P. Bentzen. "Phylogenetic Relationships of Esocoid Fishes (Teleostei) Based on Partial Cytochrome b and 16S Mitochondrial DNA Sequences." *Copeia* (2000): 420–431.

Martin-Bergmann, K. A., and J. H. Gee. "The Central Mudminnow, *Umbra limi* (Kirtland), a Habitat Specialist and Resource Generalist." *Canadian Journal of Zoology* 63 (1985): 1,753–1,764.

Mikschi, E., J. Wanzenböck, compilers. "Proceedings of the First International Workshop on *Umbra krameri* Walbaum, 1792." *Annalen des Naturhistorischen Museums in Wien Serie B Botanik und Zoologie* 97B (1995): 437–508.

Organizations

Muskies Canada Sport Fishing and Research, Inc.. P.O. Box 814, Station C, Kitchener, Ontario N2G 4C5 Canada. Web site: <http://www.trentu.ca/muskie/mc.html>

Other

"Alaska Blackfish." Alaska Department of Fish and Game, Wildlife Notebook Series [cited February 6, 2003]. <http://www.state.ak.us/local/akpages/FISH.GAME/notebook/fish/blackfsh.htm>

"Blackfish: A Cultural Mini-Unit." Alaska Native Knowledge Network [cited February 6, 2003]. <http://www.ankn.uaf.edu/UNITS/blackfish.html>

"The International Muskie Homepage." [cited February 6, 2003]. <http://www.trentu.ca/muskie/muskie.html>

"Understanding Northern Pike and Muskie." The Content Well [cited February 6, 2003]. <http://www.thecontentwell.com/Fish_Game/Northern_Pike/Pike_index.html>

Juan Andrés López, MS

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Osmeriformes

(Smelts, galaxiids, and relatives)

Class Actinopterygii
Order Osmeriformes
Number of families 9

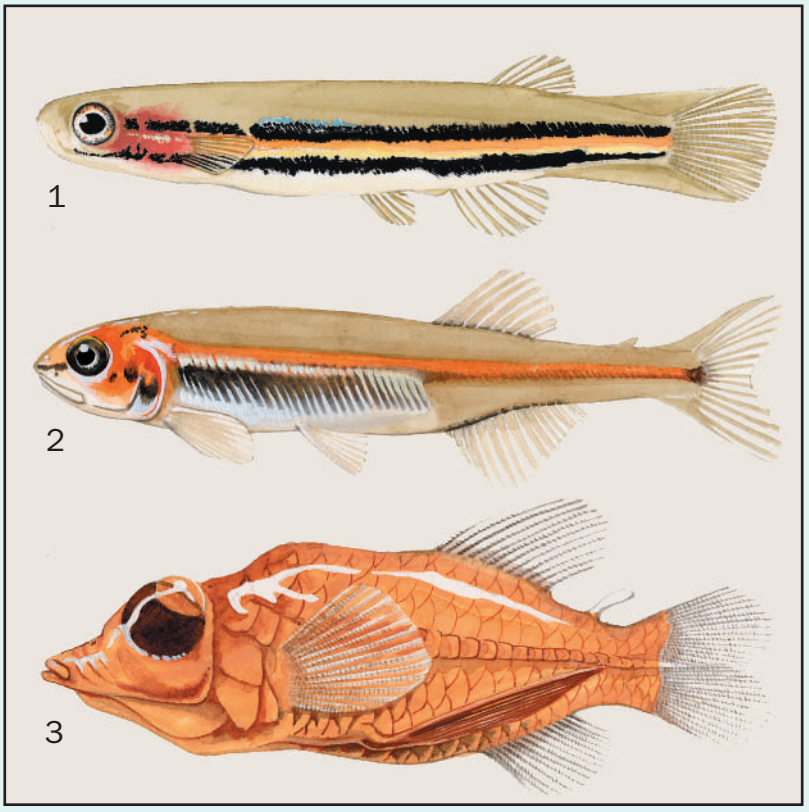


Illustration: 1. Black-stripe minnow (*Galaxiella nigrostriata*); 2. Barreleye (*Macropinna microstoma*); and 3. Australian smelt (*Retropinna semoni*). (Illustration by Jonathan Higgins)

Evolution and systematics

Fossil Osmeriformes include *Speirsaenigma lindoei*, the oldest fossil osmerid from the Paleocene formations of Alberta, Canada, and a presumed close relative of the ayu (*Plecoglossus altivelis*; suborder Osmeroidei), *Enoplophthalmus* (Osmeroidei) from Europe, and possibly the family Pattersonellidae within the Argentinoidei.

The systematics of the "lower" euteleosts, particularly the Protacanthopterygii (the pikes, salmons, and smelts), has been in a constant state of flux since about the middle of the 1970s. Many phylogenies developed since that time considered that the Protacanthopterygii included three main lineages, one that included the pikes, pickerels, and mudminnows (Esociformes), another including the salmons, trouts, chars, graylings, and whitefishes (Salmoniformes), and a third comprising the freshwater and diadromous smelts, the galaxiids, the southern graylings, the marine argentines, deep-sea smelts, barreleyes, and slickheads (Osmeriformes). The ancestor of the remaining teleosts, the "higher teleosts," or the Neoteleosti, is thought to be either the common ancestor of the Protacanthopterygii and the Neoteleosti, or to have risen within the Protacanthopterygii (Johnson and Patterson, 1996). However, many researchers did not necessarily formally recognize any of the above groups at the order level. Furthermore, the precise relationships of the various members of these groups has been a source of constant debate among ichthyologists researching the "lower" euteleosts (Johnson and Patterson [1996], as well as Rosen [1974], Fink [1984], Nelson [1994], and Begle [1991 and 1992]), who base their research primarily on anatomical and morphological data, and the most extensive study utilizing molecular data of Waters et al. (2000).

In light of the lack of consensus among these studies, it seems prudent, for the time being at least, to retain the traditional groupings/orders of the Esociformes, Salmoniformes, and Osmeriformes, while modifying them slightly to take into account the thorough studies of Johnson and Patterson (1996) and Waters et al. (2000). Such a scheme has been used in this chapter. However, it is likely that, with the collection of additional molecular data from a suite of taxa that represents all the major groupings, a further revision to the classification of the "lower" euteleostean fishes will occur.

If the classification given above is accepted, the Osmeriformes contains two suborders, the Osmeroidei (the smelts, galaxiids, etc.), which includes four families and approximately 70 species, and the Argentinoidei (the argentines, deep-sea smelts, etc.), which includes five families and approximately 170 species. Just as it is likely that changes to the classification of this group will occur with the collection

of more data, so it is also likely that the number of species will increase.

The nine families of Osmeriformes are: smelts (Osmeridae); salamanderfishes (Lepidogalaxiidae); New Zealand smelts or southern graylings (Retropinnidae); galaxiids or southern minnows (Galaxiidae); Argentines or herring smelts (Argentinidae); barreleyes or spookfishes (Opisthoproctidae); deep-sea smelts (Microstomatidae); tubeshoulders (Platytroctidae); and deep-sea slickheads or slickheads (Alepocephalidae).

Physical characteristics

Morphological characteristics that are unique to, and present in, all members of the Osmeriformes have not yet been determined, and this is reflected in the placement of the group and its constituent members at different taxonomic levels by many researchers, including Fink (1984), Eschmeyer (1990), Johnson and Patterson (1996), and Helfman et al. (1997).

It is often stated that members of this group are generally silvery and elongate fishes. However, this probably reflects the fact that most authors are more familiar with the Northern Hemisphere species of the family Osmeridae (smelts) than with other groups. For example, even though members of the Southern Hemisphere families Galaxiidae and Lepidogalaxiidae are generally elongate, only a few have a silvery belly and none could be considered silvery overall, the majority having a brownish or olive base color overlaid with stripes, spots, or mottling of various colors. In addition, although many Argentinidae possess silvery sides, many species found in the other families of the suborder Argentinoidei, and in particular those that inhabit the deep oceans, are black or brown in color. In regard to shape, most members of the order are elongate, but the Opisthoproctidae (barreleyes) are often deep bodied and laterally compressed.

Members of the Osmeriformes are usually very small to small fishes, ranging in size from 1.2 to 27.5 in (3–70 cm); 0.0016 oz to 3 lb (0.22 g–1.3 kg). The maximum length recorded for the eastern Australian galaxiid (*Galaxiella pusilla*) is only 1.5 in (3.9 cm), and the mean length of males and females at maturity is only 0.9 and 1.1 in (2.4 and 2.8 cm), respectively. However, some representatives of the argentines (Argentinidae) and slickheads (Alepocephalidae) may reach considerably larger sizes than the diminutive eastern Australian galaxiid, including the slickhead (*Alepocephalus rostratus*) of the western Mediterranean and eastern Atlantic, which attains a length of at least 27.5 in (70 cm).

There are several physical characteristics of the major groups of Osmeriformes that help to distinguish them. Helfman noted that Osmeriformes have a single dorsal fin made up of soft rays, have abdominal pelvic fins, often have an adipose fin, and generally have a toothless maxilla. The smelts (superfamily Osmeroidea) are typical osmeriforms, in that they are elongate fishes with bright silvery scales, and have a dorsal fin situated toward the center of body, as well an adipose fin and a forked caudal fin. In most species, fingerlike filaments rising from the pyloric region of the stomach (pyloric ceca) are present, these structures aid digestion. Although most osmeroids are covered with bright silvery scales, others, such as the ayu (subfamily Plecoglossinae) are olive dorsolaterally and white ventrally. An adhesive membrane that acts as an anchoring mechanism surrounds the eggs of all members of the Osmeroida, and several species smell of cucumber instead of fish.

In contrast to the predominantly silvery Osmeroidea, fishes in the superfamily Galaxioidea (galaxiids and relatives) often have a brown-to-olive base color overlaid with stripes, bands, or spots of various colors. Although members of the Retropinnidae and some species of the Galaxiidae, i.e., the single species *Lovettia sealii* (Tasmanian whitebait), and both species of *Aplochiton*, have an adipose fin and a deeply forked caudal fin, the other galaxiids and the salamanderfish (*Lepidogalaxias salamandroides*) have no adipose fin and a truncate or rounded caudal. Pyloric ceca are present in both species of *Aplochiton* and some other members of the Galaxiidae. The majority of the Galaxiidae are scaleless.

Like the Osmeroidea, most members of the superfamily Argentinoidea (argentines, deep-sea smelts, and relatives) are generally silvery, and have a dorsal fin situated toward the middle of the body and a forked caudal fin. Although some species within the Microstomatidae and the Bathylagidae (deep-sea smelts) possess an adipose fin, others do not. Most members of this group have small mouths with no teeth on the upper jaw. As is the case with many fishes that are nocturnal or inhabit deep waters, many members of the superfamilies Argentinoidea and Alepocephaloidea (slickheads and relatives) have very large eyes, an adaptation that maximizes the collection of the little light available in poorly lit waters.

Unlike the other marine, and often deep-sea, members of the Osmeriformes, such as the Argentinoidea, the Alepocephaloidea are generally black/brown in color, have a dorsal fin situated toward the back of the body, do not possess an adipose fin, and generally have large mouths that, except for the three species of *Leptochilichthyes*, have teeth on the upper jaw.

Sexual dimorphism has been recorded in some members of the osmeriforms. For example, female salamanderfish attain lengths of over 2.7 in (7 cm), but the males are much smaller and have never been recorded at lengths greater than 2 in (5 cm). Furthermore, the males develop a series of enlarged scales, or a scale sheath, around their anal fin, which is absent in females. Males of many osmerids develop tubercles during the breeding season. In addition to exhibiting sexual dimorphism with regard to differences in size, some osmeriforms develop nuptial coloration. For example, during the breeding season, some galaxiids become particularly brightly colored. The black-stripe minnow (*Galaxiella nigrostriata*) develops a bright orange to vermillion lateral stripe, which is often highlighted by the development of dark brown to black stripes on either side.

Distribution

The first suborder of the Osmeriformes, the Osmeroidei (smelts, galaxiids, etc.), is restricted to latitudes north and south of the tropics. Within this suborder, those taxa that constitute the superfamily Osmeroidea are, with the notable exception of

some members of the tribe Salangini (icefishes and noodlefishes), restricted to the cooler regions of the Northern Hemisphere. The Osmeroidea have a wide distribution, occurring in the Arctic, Atlantic and Pacific Oceans, as well as the rivers that drain into these oceans. However, they are absent from the Indian Ocean and its drainages, presumably a reflection of the fact that the vast majority of species comprising this superfamily occur in cool temperate waters. They are also absent from the Mediterranean and its drainages. The tribe Osmerini (smelts) has a circumpolar distribution, with representatives in the Arctic, Atlantic, and particularly the Pacific Oceans, but the ranges of the Plecoglossinae (the ayu, or sweetfish) and the Salangini are far more restricted; both these groups are found only in the coastal waters and drainages of the eastern Pacific. However, while the Plecoglossinae and the Salangini do not occur in the Arctic or Atlantic Oceans or their drainages, their extension into the lower latitudes is far greater than any other member of the Osmeroidei. For example, the Plecoglossinae, represented solely by the ayu, has a range that extends from northern China to Korea and Taiwan in the south; the Salangini, represented by 11 species, has a range that that has a similar northern extent of its range but extends into Vietnam.

In contrast to the Northern Hemisphere Osmeroidea, the three families in the superfamily Galaxioidea are found only in the Southern Hemisphere. The most widespread family is the Galaxiidae, representatives of which are found in Australia (where 22 of the 35 species occur), Lord Howe Island, New Caledonia, Tasmania, Chile, Argentina, and the tip of South Africa. Two of the remaining three families, the Retropinnidae and Prototroctidae, are found in Australia and New Zealand. Two species of the Retropinnidae, the Australian smelt (*Retropinna semoni*) and the Tasmanian smelt (*Retropinna tasmanica*), together have an extensive range that encompasses much of subtropical and temperate eastern Australia. The cucumberfish (*Retropinna retropinna*) and Stokell's smelt (*Stokellia anisodon*) are found in New Zealand. The Prototroctidae are represented in Australia by a single species, the Australian grayling, found in the coastal streams of New South Wales, Victoria, and Tasmania. The New Zealand grayling (*Prototroctes oxyrhynchus*) was last recorded in the 1920s. The third family of Southern Hemisphere Osmeroidei, Lepidogalaxiidae, consists of the single species, the salamanderfish, which is confined to the acid/peat flat region of the southwestern tip of Western Australia.

In contrast to the suborder Osmeroidei, whose members occur in fresh or coastal marine waters and essentially have a holarctic distribution, the obligate marine members of the suborder Argentinoidei can be found in all ocean waters from the Arctic in the north, through the Atlantic, Indian, and Pacific Oceans (including tropical and equatorial regions), to the southern ocean around Antarctica in the south. Species of the family Opisthoproctidae, subfamily Microstomatinae, are found in tropical to temperate regions of the Atlantic, Indian, and Pacific Oceans. Fishes in the subfamily Bathylaginae are represented in the subarctic to Antarctic, Atlantic, Indian, and Pacific Oceans; members of the family Argentinidae are found throughout Atlantic, Indian, and Pacific waters; and members of the families Platytroctidae and Alepocephalidae are found in all oceans.

Habitat

Osmeriforms are found in most aquatic habitats, in fresh waters in torrential mountain streams, slow-flowing rivers, ponds, lakes, and even pools that become completely dry for several months of the year, to highly variable salinity of estuaries, out into shallow inshore marine habitats, and on to the meso- and bathypelagic regions of the open ocean (deeper than 9,840 ft/3,000 m). Thus, with the exception of the freshwater systems of the lower latitudes of the Americas, Africa, the Indian subcontinent, and Australia, members of this order may be found in marine and freshwater environments off or in all of the continents. Furthermore, in the more temperate regions of the Southern Hemisphere, they are likely to be encountered in any aquatic habitat that fish biologists sample.

For example, in the fresh waters of Australia, species such as the Australian grayling and the climbing galaxias (*Galaxias brevipinnis*) tend to be restricted to the upper reaches of river systems, where they are found in shady areas over a rocky substrate in clear waters of moderate- to fast-flowing tributary streams. Other species, such as the barred galaxias (*Galaxias fuscus*), although also restricted to the headwaters of river systems, appear to prefer the slower-flowing pools below riffles and rapids. Further downstream, species such as the Australian smelt and the trout minnow (*Galaxias truttaceus*) tend to be found in the still to slow-flowing backwaters of streams and rivers, and to lakes and swamps, where they are found amid vegetation, logs, rocks, and other structure around the margins. Other species of Southern Hemisphere osmeriforms, such as swan galaxias (*Galaxias fontanus*), Clarence galaxias (*Galaxias johnstoni*), and Pedder galaxias (*Galaxias pedderensis*) are most commonly found in lakes and pools; Tasmanian mudfish (*Galaxias cleaveri*) and swamp galaxias (*Galaxias parvus*) occur in muddy marshes and swamps; and black-stripe minnow and salamanderfish inhabit small tannin-stained and acidic pools that often become completely dry in summer. Other Southern Hemisphere forms, such as the western minnow (*Galaxias occidentalis*), are found in all the above habitats, as well as in many of the brackish, salt-affected, streams, rivers, and lakes that are unfortunately becoming more common in southwestern Australia. Some populations of trout minnow and common jollytail (*Galaxias maculatus*) spend their adult lives in rivers and lakes, but move down into the brackish areas of estuaries to spawn. The larvae then move out to sea, where they spend the first year of life before moving back into rivers as juveniles.

In the Northern Hemisphere, most osmeriforms in fresh waters are usually anadromous forms on their annual spawning run, however, some species, such as the rainbow smelt (*Osmerus mordax*) of North America and ayu of Asia, have both anadromous or amphidromous and freshwater populations. Freshwater populations of both these species tend to spend their adult life in lakes.

As with the freshwater osmeriforms, the marine forms also occur in a wide range of marine habitats. The majority of the anadromous, amphidromous, and strictly marine Osmeroidea, such as the capelin (*Mallotus villosus*), are found in the shallow coastal waters out to the continental shelf, while members of

the superfamily Argentinoidei are found in these waters and also out over the continental shelf and into the open ocean. Although representatives of the Argentinoidei occur in all major habitats of the open ocean, only one species of the family Alepocephalidae, *Microphotolepis schmidti*, is known to inhabit the epipelagic zone (the top 656 ft/200 m of the water column). However, the Argentinoidei is well represented in the deeper zones of the open oceans. For example, in the Western Central Pacific Ocean (based on the FAO designation), *Nansenia ardesiaca*, *Nansenia pelagica*, and *Xenophthalmichthys* (subfamily Microstomatinae); *Bathylagus nigrigenys* and *Dolicholagus longirostris* (longsnout blackmelt, subfamily Bathylaginae); and *Dolichopteryx longipes*, *Opisthoproctus grimaldii*, *Opisthoproctus soleatus*, and *Winteria telescopa* (family Opisthoproctidae), are meso- to bathypelagic, meaning that they live in open waters above the bottom at depths of 656–13,120 ft (200–4,000 m). In the same region, *Argentina* spp. and *Glossanodon struhsakeri* (family Argentinidae) are benthopelagic, living on and just above the bottom, on the outer continental shelf and slopes to depths of about 4,590 ft (1,400 m). Approximately 59 species of the family Alepocephalidae and approximately 21 species of the family Platytroctidae are found above the continental shelf and ocean ridges, and are considered to be engybenthic, as they inhabit a layer of water that extends from just above the bottom to several feet above it. Although most of the species of the families Alepocephalidae and Platytroctidae are known from depths of 2,625–8,200 ft (800–2,500 m), a few species of the former are inhabitants of the abyssal depths, having been caught from more than 16,400 ft (5,000 m).

Not only are the osmeriforms found in a diverse array of habitats, they also live in some of the most inhospitable environments in which fishes are found. For example, fishes that live in the deep oceans, such as members of the suborder Argentinoidei, live in one of the most hostile environments on Earth, where little, if any, light visible to the human eye penetrates below 656–2,625 ft (200–800 m). Thus, deep-sea fishes, depending on the amount of light entering their domain, must either have eyes that maximize light collection or rely on other senses in such a dark environment. Furthermore, such a lack of light in the ocean depths has two major effects; first, due to the lack of the warming light, temperatures in the bathypelagic zone are 35.6–41°F (2–5°C); second, as no light enters this deep zone, photosynthesis cannot occur and phytoplankton cannot survive, thus productivity is dependent on the "rain" of dead organisms and feces from the euphotic zone (the zone of light penetration) and food is consequently scarce. Third, low productivity is one thing, but the massive volume of the ocean deep means that the little food available is spread very thinly. If these factors were not enough to create a harsh environment, the added difficulty of living in deep water, where pressure increases by one atmosphere for every increase in depth of 33 ft (10 m), cannot be underestimated. Not only are chemical reactions affected by increases in pressure, but the gas solubility in the blood and tissues and the difficulty of secreting gas into the swim bladder are also increased.

In addition to the severe environmental conditions of deep-sea environments, other osmeriforms, such as salamanderfish and black-stripe minnow, live in small, tannin-stained and acidic pools that often become completely dry in summer, habitats which are equally extreme.

Behavior

Published works describing the behavior of osmeriform species are scarce. The few that do exist generally describe the spawning migrations of the freshwater, anadromous, and coastal forms, or the migrations of juveniles of the amphidromous forms back into the rivers. For example, with the onset of winter rains, many galaxiids move upstream into tributaries and feeder streams where they spawn amongst flooded vegetation (western minnow), or on rocks (marbled galaxias, *Galaxias olidus*). During these upstream migrations, some species, such as climbing galaxias and western minnows, can "climb" obstacles as high as 33 ft (10 m) by jumping and wriggling in an eel-like fashion, using their pelvic and pectoral fins to lever themselves forward and upward. This is quite a feat, considering that individuals of these species are rarely larger than 6 in (15 cm). Species that have amphidromous populations, such as the common jollytail, undertake migrations. The adults move downstream to spawn in estuaries, the larvae that result then move out to sea before returning to the rivers in large schools of so-called whitebait. The spawning migrations of the amphidromous, anadromous, and coastal forms are described in the species descriptions of the ayu, eulachon, and the capelin, respectively.

Virtually nothing is known about the behavior of the deep-sea osmeriforms. However, two behavior patterns are likely in at least some species. First, most mesopelagic fishes undergo vertical feeding migrations, in which they move to the epipelagic zone at night to feed on the abundant zooplankton found in this region. Such migrations have been recorded for at least one species within the Argentinoidea, the longsnout blacksmelt (*Dolicholagus longirostris*), so it is likely that other species also undertake such daily migrations. Second, many species of deep-sea fishes have bioluminescent light-emitting organs called photophores, which are thought to be used for attracting mates (by flashing in particular pulse patterns), for attracting prey items, and for "hiding" the fishes from predators. The latter mechanism is thought to work in those species that live in regions into which some light just penetrates, whereby rows of photophores along the ventral surface reduce the chance that the fish is silhouetted when viewed from below.

Feeding ecology and diet

Although some representatives from most groups, including the capelin and the slender argentine (*Microstoma microstoma*), prey predominantly on small benthic and pelagic arthropods, others, such as the surf smelt (*Hypomesus pretiosus*) and European smelt (*Osmerus eperlanus*), have much wider diets, ingesting arthropods, fishes, mollusks, and worms. The Agassiz's slickhead (*Alepocephalus agassizii*) feeds on crustaceans, worms, echinoderms, and comb jellies. Other species of osmeriforms are, or become, specialist feeders. The mirrorbelly (*Opisthoproctus grimaldii*) is reported to feed on the

stinging cells and tentacles of jellyfishes, and others, such as the ayu and black-stripe minnow, both exhibit marked shifts in diet at the end of their larval/juvenile stages.

Osmeriformes are preyed on by a wide variety of predators. For example, sharks, as well as a variety of bony fishes, seals, birds, and dolphins, have been reported to prey on the eulachon (*Thaleichthys pacificus*); bony fishes and squids prey on the argentines.

Reproductive biology

Fishes in the suborder Osmeroidei, such as the surf smelt and capelin, show a diverse array of breeding strategies, undergoing extensive migrations from coastal seas to surf beaches and estuaries, where they often form massive spawning aggregations, males pressing against females until they release their eggs, the males then releasing their sperm. The eggs are then fertilized and wave action buries them below the sand. Other members of the Osmeroidei, such as the eulachon and ayu, move up into rivers to spawn. Freshwater populations of Northern Hemisphere osmeroids tend to undergo similar spawning migrations, and may spawn in habitats similar to those of the migratory forms, such as the ayu. They may also spawn in different habitats. The freshwater forms of the European smelt tend to spawn in lakes, the anadromous forms spawn in rivers.

Within the Southern Hemisphere osmeroids, the Tasmanian smelt is anadromous, spending most of its life in the sea before returning to estuaries and rivers to spawn. In other species, such as the common jollytail, most populations are amphidromous. The adults of this species live in fresh water, but during autumn move downstream to spawn in estuaries. Spawning takes place on spring tides amid inundated vegetation, the eggs developing out of water and hatching two weeks later on the next spring tide. The larvae are then washed out to sea, where they feed and develop into juveniles before returning to the rivers to complete their life cycle. In purely freshwater forms such as the western minnow, migrations into tributaries or into the shallows of lakes are usual.

Within the Argentinoidei, stout blacksmelt (*Pseudobathylagus milleri*), and the longsnout blacksmelt produce planktonic eggs and larvae, and it is likely that other members of this suborder do likewise. Little other data are available on the reproductive behavior in the deep-sea osmeriforms.

The age at first maturity, whether the adults survive to spawn in more than one year, and the spawning pattern, spawning period, and number and size of eggs vary greatly within the order. For example, anadromous forms of the European smelt do not spawn until their third or fourth year, when during a short breeding season of one to three months they produce 8,000 to 50,000 small (0.02–0.03 in/0.06–0.09 cm) demersal eggs. Adults usually die after spawning. Other species, such as the mudminnow (*Galaxiella munda*), which becomes mature at the end of its first year of life, has a spawning period that extends for three to four months, during which they produce several small batches (37–92) of smallish (0.06–0.05 in/0.09–0.14 cm) demersal eggs. Most mudminnow die within one or two months of spawning. Unlike the above two species, the western minnow spawns at the end of its first year and can live to spawn a further four times.

The salamanderfish is unique in the Osmeriformes in that, rather than broadcasting its eggs and sperm, it undergoes internal fertilization.

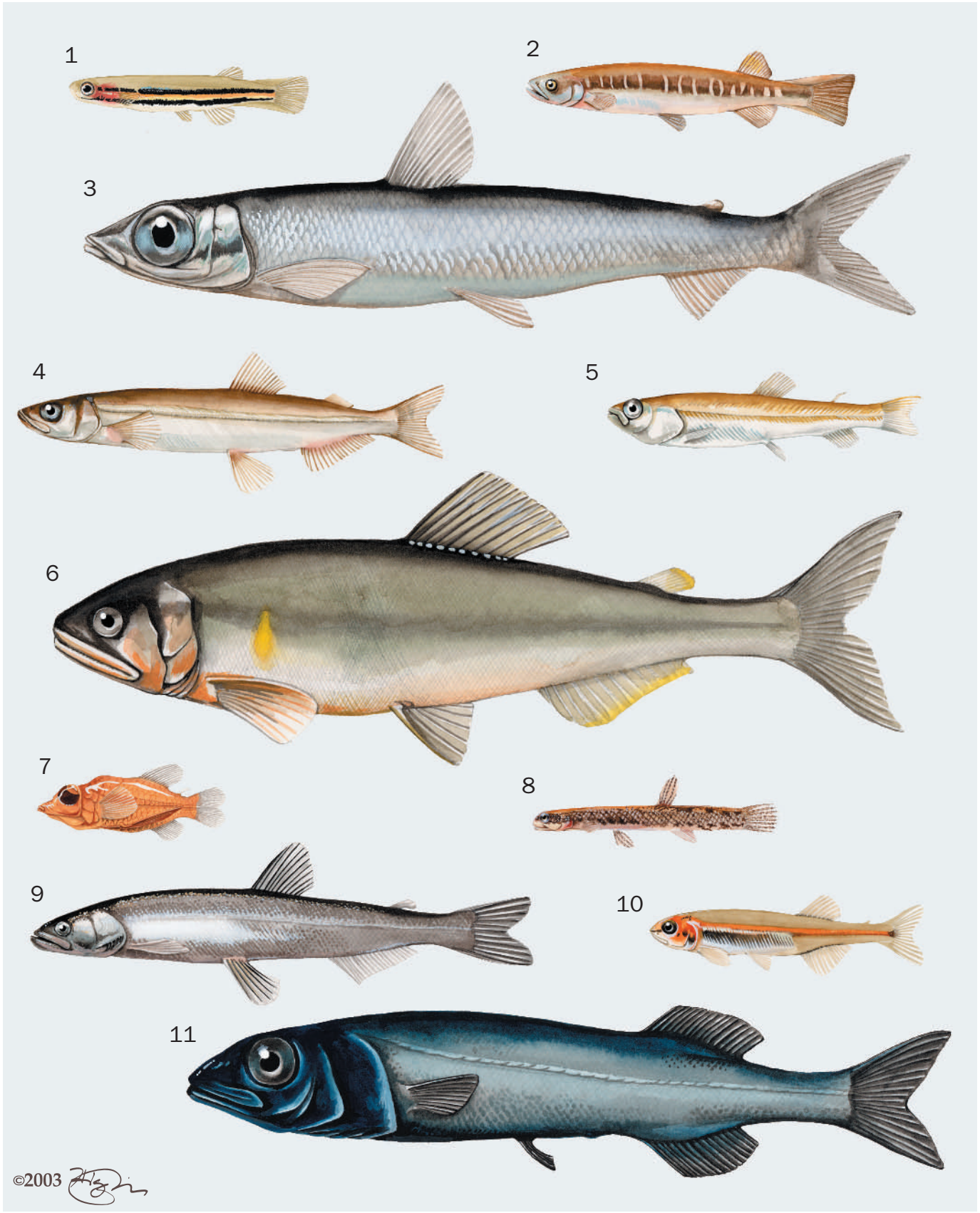
There are no reports of parental care in the Osmeriformes.

Conservation status

Eight species of Osmeriformes are listed by the IUCN. One species is classified as Extinct, one species as Endangered, one species as Critically Endangered, three species as Vulnerable, and two species as Data deficient. In addition, many Australian forms are considered by the Australian Society for Fish Biology to be data deficient to endangered, largely because of land clearing and the subsequent degradation of freshwater habitats. Many deep-sea forms are small and rare, and thus are likely to be overlooked by conservationists.

Significance to humans

Due to their generally small size and/or inaccessibility (in deep-sea forms), most Osmeriformes are of little importance to humans, either commercially or recreationally. However, in the Northern Hemisphere, eulachon, capelin, European smelt, and ayu form the basis of important local commercial and recreational fisheries during their spawning migrations, and in the Southern Hemisphere, the juveniles of the anadromous species, such as the Tasmanian whitebait and common jollytail, form the basis of important commercial whitebait fisheries in New Zealand and Chile. In Australia, massive falls in whitebait capture during the 1970s led to the closure of the fishery. However, it has since been reopened as a tightly regulated recreational fishery.



1. Black-stripe minnow (*Galaxiella nigrostriata*); 2. Western minnow (*Galaxias occidentalis*); 3. Greater argentine (*Argentina silus*); 4. Capelin (*Mallotus villosus*); 5. California smoothtongue (*Leuroglossus stilbius*); 6. Ayu (*Plecoglossus altivelis*); 7. Barreleye (*Macropinna microstoma*); 8. Salamanderfish (*Lepidogalaxias salamandroides*); 9. Eulachon (*Thaleichthys pacificus*); 10. Australian smelt (*Retropinna semoni*); 11. California slickhead (*Alepocephalus tenebrosus*). (Illustration by Jonathan Higgins)

Species accounts

California slickhead
Alepocephalus tenebrosus

FAMILY
Alepocephalidae

TAXONOMY
Alepocephalus tenebrosus Gilbert, 1892, Santa Barbara Channel, California, United States, 359–822 fathoms (2,154–4,932 ft/655–1,500 m).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length about 23.6 in (60 cm), moderately sized, fusiform, laterally compressed; dorsal fin posteriorly placed; adipose fin absent. Skull translucent, body brown to black. Swim bladder absent.

DISTRIBUTION
North Pacific from Bering Sea to California; southeastern Pacific, Chile.

HABITAT
Marine. Deep waters, oceanic at depths 150–18,045 ft (46–5,500 m).

BEHAVIOR
Little is known about the biology and behavior. However, other slickheads are gregarious, forming large schools close to the bottom.

FEEDING ECOLOGY AND DIET
Larvae and juveniles ingest benthic and planktonic crustaceans. Others feed on squids, arrow worms, comb jellies, and other deep-sea fishes such as anglerfishes.

REPRODUCTIVE BIOLOGY
Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not commercially sought after due to soft texture. ◆

Greater argentine
Argentina silus

FAMILY
Argentinidae

TAXONOMY
Salmo silus Ascanius, 1775, Bergen, Norway.

OTHER COMMON NAMES
English: Atlantic argentine; French: Grande argentine, saumon doré; German: Goldlachs; Spanish: Pez plata, sula.

PHYSICAL CHARACTERISTICS
Standard length about 27.5 in (70 cm), moderately sized, elongate; dorsal fin medially to anteriorly placed, anterior to origin of pelvic fins. Adipose fin present. Brown to olive dorsally, silver laterally and ventrally. Mouth small, and lacks teeth on jaws.

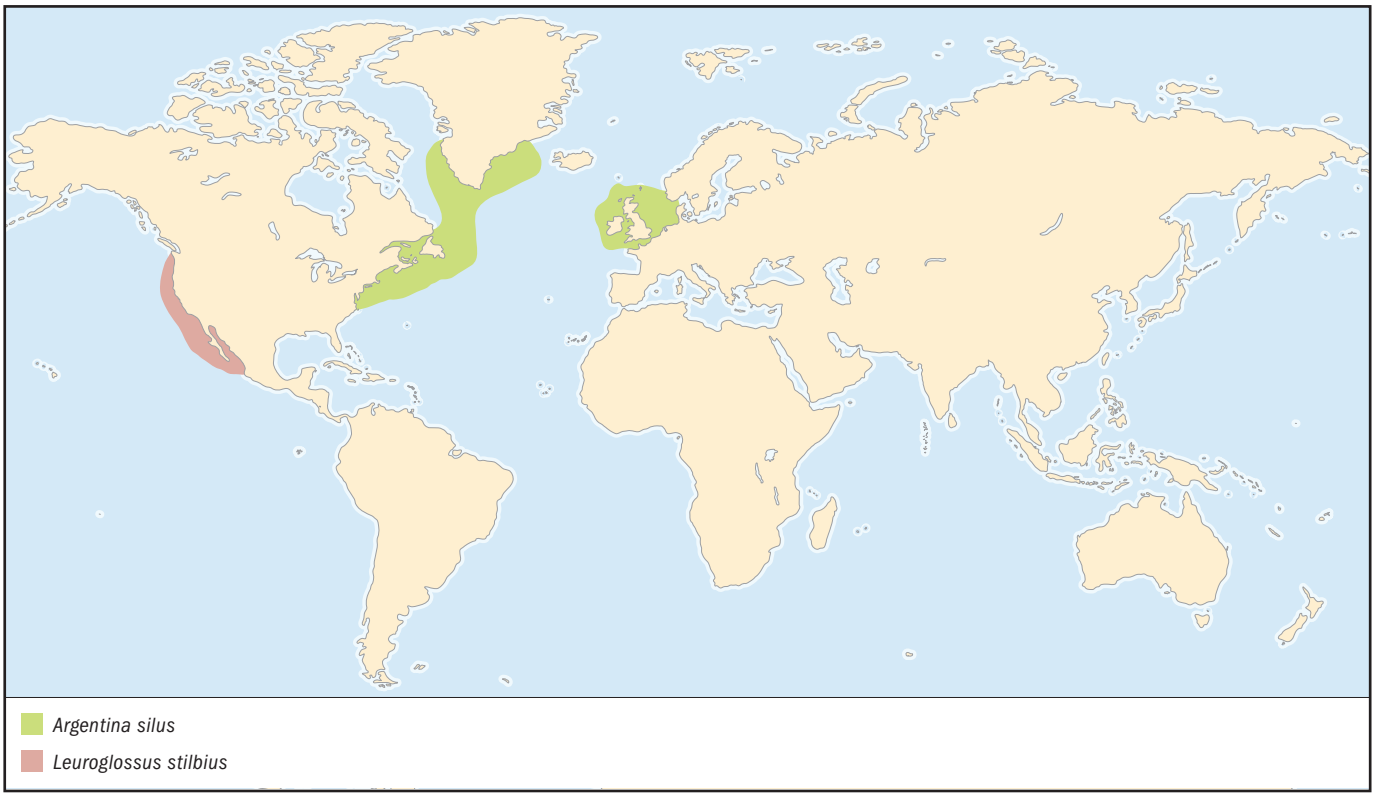
DISTRIBUTION
Western Atlantic, from Davis Strait in the north, to Georges Bank in the south. Eastern Atlantic from Denmark Strait to west coast of Scotland and deeper parts of the North Sea.

HABITAT
Marine. Deep waters, oceanic at depths of 460–4,725 ft (140–1,440 m).

BEHAVIOR
Gregarious, forms large schools close to the bottom.

FEEDING ECOLOGY AND DIET
Feeds on benthic and planktonic crustaceans, squids, arrow worms, and comb jellies. Preyed upon by bony fishes, such as swordfishes and hakes, and seals.

REPRODUCTIVE BIOLOGY
Attains sexual maturity at the end of the fourth year. Spawns in late winter off Canada, and in April and May in the North Sea. Eggs and larvae are pelagic. Juveniles settle on the bottom of waters up to about 410 ft (125 m) deep before moving out into deeper water.



CONSERVATION STATUS
Not listed by the IUCN. May be particularly susceptible to overfishing because they have a fairly long population doubling time of between 4.5 and 14 years.

SIGNIFICANCE TO HUMANS
A commercial fishery was started by Russia in 1963, joined by Japan in 1968. Estimated sustainable yield is 5,500–24,250 tons (5,000 to 20,000 metric tons). ◆

Western minnow
Galaxias occidentalis

FAMILY
Galaxiidae

TAXONOMY
Galaxias occidentalis Ogilby, 1900, streams south of Perth, Western Australia.

OTHER COMMON NAMES
English: Western galaxias.

PHYSICAL CHARACTERISTICS
Length about 7.9 in (20 cm), small, elongate, scaleless; dorsal fin posteriorly placed. Olive green dorsally, fading to cream/white ventrally. Dark lateral bars often present.

DISTRIBUTION
Restricted to the southern corner of Western Australia, from approximately 155 mi (250 km) north of Perth to 50 mi (80 km) east of Albany.

HABITAT
Fresh waters in streams, rivers, lakes, and ponds/pools; also in brackish habitats. Schools amid riparian vegetation and open waters at all depths.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
During the day most food eaten is from the water surface (e.g., flying insects and spiders), although insect larvae and small crustaceans from the substrate and within the water column are also taken. At night switches diet to freshwater shrimps.

REPRODUCTIVE BIOLOGY
Attains sexual maturity at the end of the first year at about 2.9 in (7.5 cm). Breeding occurs during wet winter months between June and September, peaks in August (winter). Migrates into creeks or the inundated shores of lakes to spawn. Mean number of mature eggs is 905; diameter of mature eggs is 0.05 in (0.13 cm). Can live up to five years and will spawn at the end of each of these years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Fishers use them as bait for introduced trouts and European perches. ◆

Black-stripe minnow
Galaxiella nigrostriata

FAMILY
Galaxiidae

TAXONOMY
Galaxias pusillus nigrostriatus Shipway, 1953, a small drain running into Marbellup Creek on a property owned by Mr. Byland, Elleker, near Albany, Western Australia.

OTHER COMMON NAMES
German: Schwartzstreifen-Zwerggalaxie.

PHYSICAL CHARACTERISTICS
Total length about 2 in (5 cm), tiny, elongate, scaleless; dorsal fin posteriorly placed. Between June and September, adults develop nuptial coloration of two longitudinal black stripes separated by a brilliant yellow (in light-colored waters) to red stripe (in dark-colored waters). In dark-colored waters, the dorsal-most black stripes extend upward and meet. Larvae show the same nuptial coloration. Outside breeding season, color is uniform brown to black, with a faint dull-yellow to red lateral stripe.

DISTRIBUTION
Restricted to a small area of peat flats on the southern coast of Western Australia, from Augusta in the west (about 220 mi/350 km south of Perth) to Albany in the east. Two disjunct populations about 125 mi and 250 mi (200 and 400 km) to the north were found in the 1990s, suggesting that the loss of habitat caused by massive urban and rural development during the previous hundred years had a significant impact.

HABITAT
Fresh waters in streams, ponds, and shallow pools. Most commonly found in highly tannin-stained and acidic ephemeral pools, in which salamanderfish also occur. Small schools found amid riparian vegetation and open waters and at all depths.

BEHAVIOR
Estivates when pools become dry in summer. Large numbers are found in even the smallest pools (11.8 in/30 cm diameter) before they completely dry up. When pools were filled artificially, black-stripe minnow and salamanderfish emerged from the substrate within two hours. Unlike salamanderfish, does not apparently have any specific anatomical, physiological, or behavioral adaptations to aid estivation, and must presumably survive in crustacean burrows (and similar) that contain water through the dry season.

FEEDING ECOLOGY AND DIET
Active carnivores at all stages. The smallest larvae, 0.19–0.43 in (0.5–1.1 cm), feed predominantly on rotifers; larger larvae, 0.5–0.9 in (1.2–2.3 cm) consume fewer rotifers, but far more small crustaceans and insect larvae. Juveniles and adults continue to take crustaceans and insect larvae, but a large part of their diet consists of terrestrial insects and spiders taken from the surface. Larvae and small juveniles assume a head-down, tail-up stance (between 30 and 45°), forming their body into an "S" shape as prey approaches, striking at high speed when the prey is within about half a body length.

REPRODUCTIVE BIOLOGY
Sexually mature at the end of the first year, when males are about 1.3 in (3.3 cm) and females 1.4 in (3.7 cm). Individuals spawn several times between June and September, peak activity in late June/early July. Mean number of mature eggs is 62; diameter is 0.03 in (0.07 cm). Most adults die within two months of spawning.

CONSERVATION STATUS
Not listed by the IUCN. Regarded as vulnerable by the Australian Society for Fish Biology.

SIGNIFICANCE TO HUMANS
The Western Australian Department of Fisheries and commercial breeders of ornamental fishes are considering its suitability as an aquarium fish. ◆

Salamanderfish
Lepidogalaxias salamandroides

FAMILY
Lepidogalaxiidae

TAXONOMY
Lepidogalaxias salamandroides Mees, 1961. Tiny creek about 6 mi (9.6 km) east-northeast of Shannon River, Western Australia.

OTHER COMMON NAMES
English: Shannon mudminnow; German: Salamanderfisch.

PHYSICAL CHARACTERISTICS
Length about 2.9 in (7.5 cm), small, elongate; dorsal fin posteriorly placed. Scales absent on head, back, and belly. Pelvic fins well developed, even at hatching. Males have enlarged anal fin sheathed with scales. Brown to gray overall, dark saddlelike markings dorsally, and blotches laterally, the latter forming a pair of stripes during breeding.

DISTRIBUTION
Restricted to a small area of peat flats on the southern coast of Western Australia. Used to extend from Margaret River in the west (about 186 mi/300 km) south of Perth) to Albany in the east; in 2003 its range had contracted to central 93–125 mi/150–200 km) of this area.

HABITAT
Fresh waters in streams, ponds, and shallow pools. Most common in ephemeral, tannin-stained, highly acidic (pH 3.0) pools that can exceed 95°F (35°C) in summer. Solitary and benthic,

rests on pelvic fins amid riparian vegetation and in open waters. Larvae and juveniles most common in very shallow water (less than 3.9 in/10 cm), tend to move into deeper waters (usually less than 39.4 in/1 m) as they grow.

BEHAVIOR
Exhibits several behaviors rare among fishes. Like lungfishes, estivates when pools in which they live become dry, burrowing into the substrate, forming an "S" shape, and producing a mucous cocoon, emerging when pools refill with winter rain. Unlike black-striped minnow, buries itself before the pool becomes almost dry.

FEEDING ECOLOGY AND DIET
Active carnivore at all stages, feeds on small crustaceans and insect larvae. Individuals rest on the substrate with their head and body raised up, supported by the large pelvic fins present at hatching. Unlike any other species of fishes, salamanderfish have very large gaps between the vertebrae immediately behind the head. These gaps allow them to move their head from side to side when scanning for prey, which is crucial, as muscles that allow movement of the eyes are absent or greatly reduced. When prey are within about half a body length, darts forward, engulfing and swallowing prey whole.

REPRODUCTIVE BIOLOGY
About 27% attain sexual maturity and spawn at the end of the first year, when males are 1.5 in (3.9 cm) and females are about 1.7 in (4.3 cm). All two-year-old fishes mature and spawn. Each individual spawns several times between late May and late August, peak activity in late July/early August. Mean number of mature eggs is approximately 82; diameter is 0.07 in (0.18 cm). Many fish survive to spawn in two seasons, but only a few survive to spawn at the end of the third and fourth years. Spawning behavior is unique. Males develop an enlarged anal fin surrounded by a sheath of scales. On finding a receptive female, a male will approach and nudge her sides, if she does not swim away or react aggressively, he will approach from the side, and using his scale sheath grasp the female around her anal fin and cloaca. Sperm is introduced into the female via his enlarged anal fin. In the laboratory, males may remain attached to a female for several hours. When physically removed, a male always reattaches from the same side; apparently, just like humans, salamanderfish are either right or left "handed."

CONSERVATION STATUS
Not listed by the IUCN. Regarded as vulnerable by the Australian Society for Fish Biology.

SIGNIFICANCE TO HUMANS
None, although the Western Australian Department of Fisheries and commercial breeders of ornamental fishes are considering its suitability as an aquarium fish. ◆

California smoothtongue
Leuroglossus stilbius

FAMILY
Microstomatidae

TAXONOMY
Leuroglossus stilbius Gilbert, 1890, Pacific off northwestern Mexico, Albatross sta. 2997, 221 fathoms (1,326 ft/400 m).

OTHER COMMON NAMES
English: Esperlan, smoothtongue, southern smoothtongue; Spanish: Esperlan, esperlan de lengua suave.

PHYSICAL CHARACTERISTICS
Length about 7.9 in (20 cm), small to moderately sized, elongate; dorsal fin medially placed; adipose fin present; eyes large. Body light to dark, may be silvery.

DISTRIBUTION
Eastern Pacific from Oregon, United States, in the north, to Gulf of California, Mexico, in the south.

HABITAT
Marine. Deep waters, oceanic at depths between surface and 2,265 ft (690 m).

BEHAVIOR
Gregarious, forms large schools.

FEEDING ECOLOGY AND DIET
Benthic and planktonic crustaceans, worms, and tunicates have been recorded in the guts of juveniles. Reported to be preyed upon by tunas off the coast of the United States. Likely to have specialized eyes as those of some close relatives. Eyes are positioned on the top of the head to increase binocular vision, and in each eye a gap in front of the lens increases illumination of the retina, which itself has specialized photoreceptors. These specializations ensure great visual sensitivity in the forward plane and spatial perception, attributes particularly relevant when searching for prey in dim environments.

REPRODUCTIVE BIOLOGY
Spawning occurs in the California Current between December and May. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Barreleye
Macropinna microstoma

FAMILY
Opisthoproctidae

TAXONOMY
Macropinna microstoma Chapman, 1939, northeastern Pacific, 53°50"00"N, 134°20"00", 2,950–2,300 ft (900–700 m) wire out.

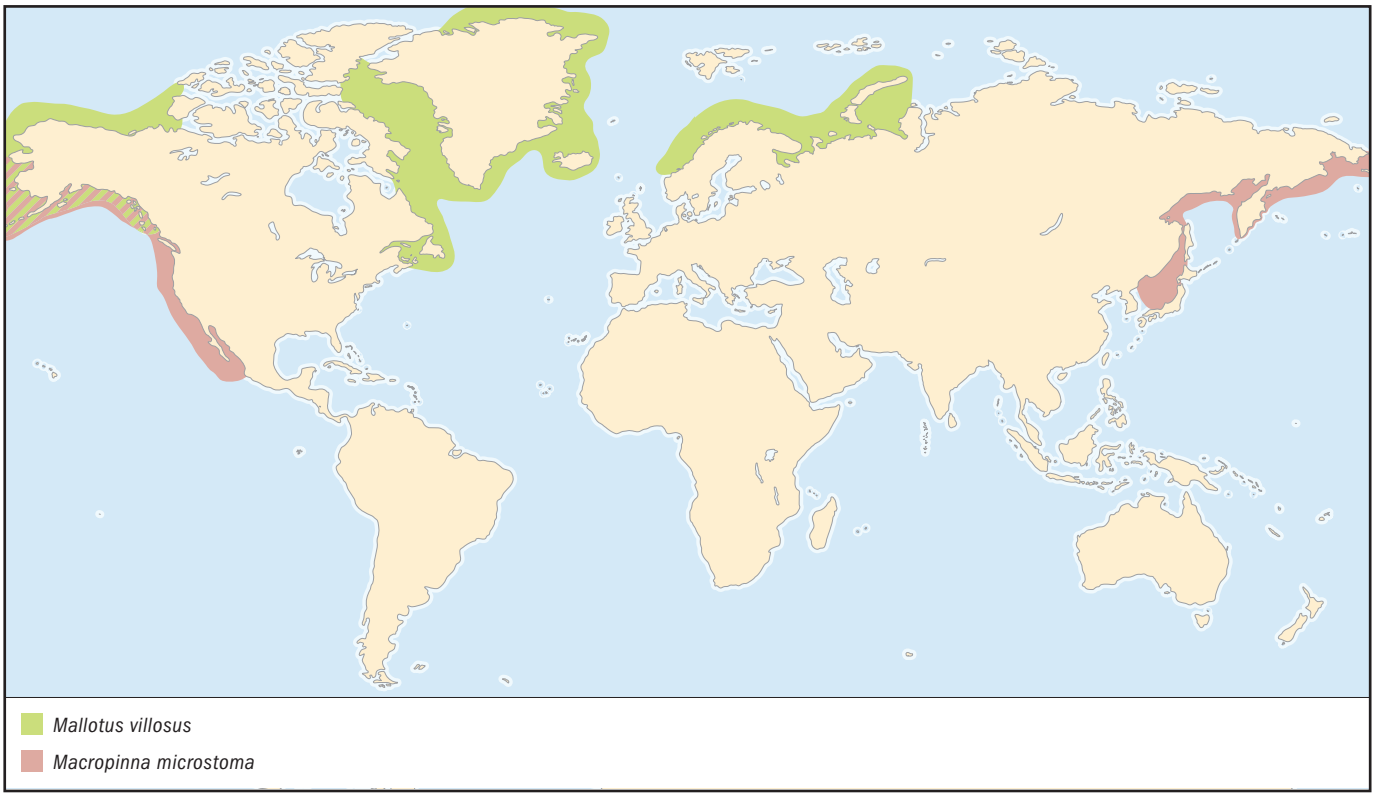
OTHER COMMON NAMES
English: Pacific barreleye; Japanese: Demenigisu.

PHYSICAL CHARACTERISTICS
Length about 1.8 in (4.5 cm). Small, deep-bodied, laterally compressed; dorsal fin posteriorly placed; adipose fin present. Eyes telescopic and large. Head clear, body black dorsally and ventrally, may be silver laterally.

DISTRIBUTION
North Pacific from Bering Sea in the north to Japan and Mexico in the south.

HABITAT
Marine. Deep waters, oceanic at depths about 330–2,950 ft (100–900 m).

BEHAVIOR
Nothing known.



FEEDING ECOLOGY AND DIET
Not much is known. Other barreleye feed on stinging cells of jellyfishes. Each stalked eye in the closely related brownsnout spookfish (*Dolichopteryx longipes*) has two retinas, one directly below the lens, the other to the side of the lens. The first retina contains a golden to silvery pigment that ensures any light is reflected backward and forward, passing through photoreceptors several times before its energy is expended, and thus maximizing the efficiency of the eye. The second retina, although not as efficient, permits the barreleye to distinguish the movement of brightly lit objects, and thus see prey from below. Due to the excellent binocular vision provided by these tubular eyes, the barreleye can determine position precisely, and can also see predators that may be approaching from its side. Such optic specializations thus aid in both feeding and predator avoidance.

REPRODUCTIVE BIOLOGY
Larvae, and probably eggs, are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Capelin
Mallotus villosus

FAMILY
Osmeridae

TAXONOMY
Mallotus villosus Muller, 1776, Iceland.

OTHER COMMON NAMES
English: Whitefish, lodde; French: Capelan atlantique; German: Lodde; Spanish: Capelan.

PHYSICAL CHARACTERISTICS
Total length about 9.8 in (25 cm). Small, moderately deep bodied; dorsal fin medially placed; adipose fin with long base. Body covered in small scales. Olive dorsally, silver laterally and ventrally. Enlarged pectoral and anal fins; two ridges of enlarged scales along each side of body in breeding males.

DISTRIBUTION
Circumpolar in the Arctic, North Atlantic, and North Pacific Oceans.

HABITAT
Marine. Oceanic moving into coastal seas to spawn. Found down to about 985 ft (300 m).

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
All stages feed on zooplankton and small benthic organisms such as euphausiid shrimps, copepods, amphipods, and worms. Predators such as rays, a range of bony fishes, seabirds, seals, whales, and dolphins take an estimated 3.3 million tons (3 million metric tons) in the northwest Atlantic.

REPRODUCTIVE BIOLOGY
Forms massive spawning aggregations over shallow banks. Spawns over a two to three month period between March and October, depending on location. Two males flank and hold a female with enlarged fins and scale ridges until she releases her

eggs, they then release the sperm. Females release up to 12,000 adhesive eggs. Many individuals survive to spawn in more than one year, although most spawning animals are in year three or four. Many fish spawning along shorelines, particularly males, become stranded on beaches and die.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Very important in commercial, recreational, and traditional fisheries throughout the range. In 1998 the commercial fishery in the northwest Atlantic was estimated at 121,000 tons (110,000 metric tons). Marketed fresh, frozen, salted, dried, smoked, as fish meal (males), and roe (females). ◆

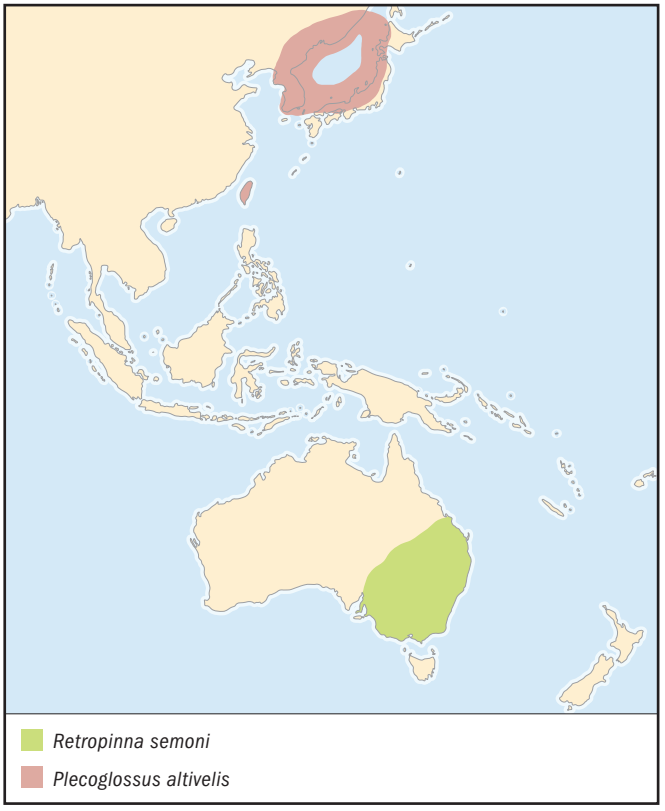
Ayu
Plecoglossus altivelis

FAMILY
Osmeridae

TAXONOMY
Salmo (Plecoglossus) altivelis Temminck and Schlegel, 1846, Japan.

OTHER COMMON NAMES
English: Ko-ayu, sweetfish; French: Ayu; Japanese: Koayu.

PHYSICAL CHARACTERISTICS
Length about 11.8 in (30 cm). Small, moderately deep bodied; dorsal fin medially placed; adipose fin present. Body covered in small scales. Olive dorsolaterally, white ventrally.



DISTRIBUTION
Coastal seas and rivers in Japan, China, Korea, and Taiwan.

HABITAT
Marine, brackish, and fresh waters. Amphidromous, demersal in coastal seas, estuaries, rivers, streams, and lakes to a depth of about 33 ft (10 m). Landlocked forms also exist. In rivers and lakes appears to prefer clear waters.

BEHAVIOR
Except for feeding and reproduction little is known regarding specific behavior patterns. In rivers, form territories, which they guard by attacking and nipping other ayu.

FEEDING ECOLOGY AND DIET
Larvae and juveniles feed primarily on small benthic crustaceans such as copepods and amphipods. Juveniles of the amphidromous form move into fresh waters in winter and spring, moving up into the higher reaches of rivers and streams. Adults use specially modified jaws and teeth to scrape algae from rocks. Adults have also been reported to eat small pebbles, although it seems likely that these were inadvertently ingested while grazing on algae. The few adults that survive spawning and return to the sea have been reported to feed on zoobenthos.

REPRODUCTIVE BIOLOGY
Sexual maturity usually attained at end of first year at about 7.9–11.8 in (20–30 cm). Spawns in freshwater during autumn, when adults move downstream to the spawning grounds. At night, excavates small pits in sand or gravel banks into which about 10,000 adhesive eggs (0.04 in/0.1 cm) are released. Eggs hatch 14–20 days later. Larger individuals spawn once, after which most die; smaller individuals have about a 50% chance of surviving to spawn again two weeks later.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Ayu form important commercial, aquaculture, recreational, and traditional fisheries. In Japan the commercial fishery and aquaculture accounted for 16,500 tons (15,000 metric tons) and 8,820 tons (8,000 metric tons), respectively, in 1979. Sport fishing in Japan involves baited hooks, flies, as well as a traditional method. In the traditional method, an ayu that has a small free-swinging treble hook fastened to it is attached to the line. Anglers swing the attached fish to ayu guarding territory, and when the resident fish nips the back of the "invader" it is caught on the free-swinging hook. In Japan the ayu forms the basis of the cormorant fishery, whereby cormorants are trained to dive for fish. This fishery is believed to date back at least 2,500 years, but is now for tourists. ◆

Eulachon
Thaleichthys pacificus

FAMILY
Osmeridae

TAXONOMY
Salmo (Mallotus?) pacificus Richardson, 1836, Columbia River, no higher than Katpootl, northwestern United States.

OTHER COMMON NAMES
English: Candlefish, oilfish, fathom fish, hooligan; French: Eulachon.

PHYSICAL CHARACTERISTICS
Total length 11.8 in (30 cm), small, slender bodied; dorsal fin medially placed; adipose fin present. Body covered in small scales. Brown to blue dorsally, silver laterally, white ventrally. Raised ridge along middle of body; large tubercles on fins of breeding males are absent or small in females.

DISTRIBUTION
Northwest Pacific between 61° and 36°N. From west of Saint Matthew Island and Kuskokwim (Bering Sea) in the north to Monterey Bay in northern California in the south.

HABITAT
Marine, brackish, and fresh waters. Anadromous, found in coastal seas, estuaries, rivers, and streams to a depth of 2,050 ft (625 m). Landlocked forms exist.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
All stages feed on zooplankton and small benthic crustaceans such as mysid and euphausiid shrimps, as well as copepods and amphipods. Adults do not feed in freshwater. Reported to be preyed upon by dogfishes, salmonids, cods, flatfishes, sturgeons, seagulls, seals, and porpoises.

REPRODUCTIVE BIOLOGY
Sexual maturity is attained at end of third year. Spawning migrations from the sea to rivers occur when river temperatures rise above 40°F (4.4°C), spawns in spring after the ice melt. Sticky eggs with a short stalk are broadcast over sand or gravel. Larvae hatch after about 30 days and are swept downstream and out to sea. Most adults die following spawning, a few survive for five years. Adults may return to natal streams to spawn.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Traditionally an important fishery for Native Americans for food and oil. Fish are so oily they were dried and used as candles. Used as food for minks and other animals farmed for fur. ◆

Australian smelt
Retropinna semoni

FAMILY
Retropinnidae

TAXONOMY
Prototroctes semoni Weber, 1895, Burnett River, Queensland, Australia.

OTHER COMMON NAMES
German: Australischer Stint; Polish: Rakietniczka semona.

PHYSICAL CHARACTERISTICS
Total length 3.9 in (10 cm), small, elongate; dorsal fin posteriorly placed; adipose fin present. Scales absent on head. Olive green dorsally, golden to orange or purple laterally, silvery ventrally. Fins enlarged in breeding males. Has only a left gonad. Often smells of cucumber when fresh.

DISTRIBUTION
Widespread in coastal drainages of southeastern Australia, from the Fitzroy River in southern Queensland to eastern South Australia; also in the Cooper Creek drainage of Lake Eyre.

HABITAT
Slow-flowing streams and rivers, lakes, and ponds/pools; also in brackish habitats. Schools among riparian vegetation and open waters at all depths.

BEHAVIOR
Gregarious, forms large schools from midwater to the surface in large open waters.

FEEDING ECOLOGY AND DIET
Feeds on insects, microcrustaceans, and algae. An important component of the diets of other fishes.

REPRODUCTIVE BIOLOGY
Sexual maturity usually attained at end of first year at about 2–3.9 in (5–10 cm). Some fish from inland and northern drainages may reach maturity in 9–11 months and at less than 1.6 in (4 cm). Spawns in fresh waters during spring. Spawning individuals develop nuptial tubercles on scales and fin rays. Releases 100–1,000 adhesive eggs (0.03 in/0.08 cm) over the streambed and/or aquatic vegetation. Larvae of about 0.18 in (0.45 cm) hatch after 10 days. Coastal populations may be amphidromous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Introduced to Tasmania as forage for introduced trouts.

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Howard Stamper Gill, PhD

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Salmoniformes
(Salmons)

Class Actinopterygii
Order Salmoniformes
Number of families 1

Photo: Sockeye salmon (*Oncorhynchus nerka*) in spawning area of Alaska, USA. (Photo by Animals Animals ©Victora McCormick. Reproduced by permission.)

Evolution and systematics

Salmoniform fossils are known from the Upper Cretaceous (about 100 million years ago) until the Pleistocene (about 11,000 years ago), mostly from North America and Europe. This order possesses several primitive anatomical features representative of an early stage in the evolution of modern bony fishes. There have been a number of systematic arrangements for this group, ranging from a single order with a single family (Salmonidae), to two orders with several families (see, for example, Johnson and Patterson 1996). For the purpose of this chapter, we will follow Nelson (1994), who considers the Salmonidae the only family for this order, with 3 subfamilies, 11 genera, and 66 species.

Physical characteristics

The largest of the salmoniform fishes are the Chinook salmon (*Oncorhynchus tshawytscha*) and the Danube and Siberian huchens (*Hucho hucho*) both about 59 in (1.5 m) in length, with the former weighing up to 136 lb (62 kg). As expected from such strong swimmers, the salmoniform body and fins are streamlined and symmetrical, being covered with small and smooth cycloid scales. All fins have soft rays. They have a small, fleshy adipose fin (which is a primitive character) located between the dorsal fin and the powerful caudal fin. The dorsal fin is located midway along the body; the paired pectoral fins are ventral and located directly posterior to the head. They also have a pair of pelvic fins directly beneath the dorsal fin, and a single anal fin located beneath the adipose fin. The swim bladder is connected to the gut.

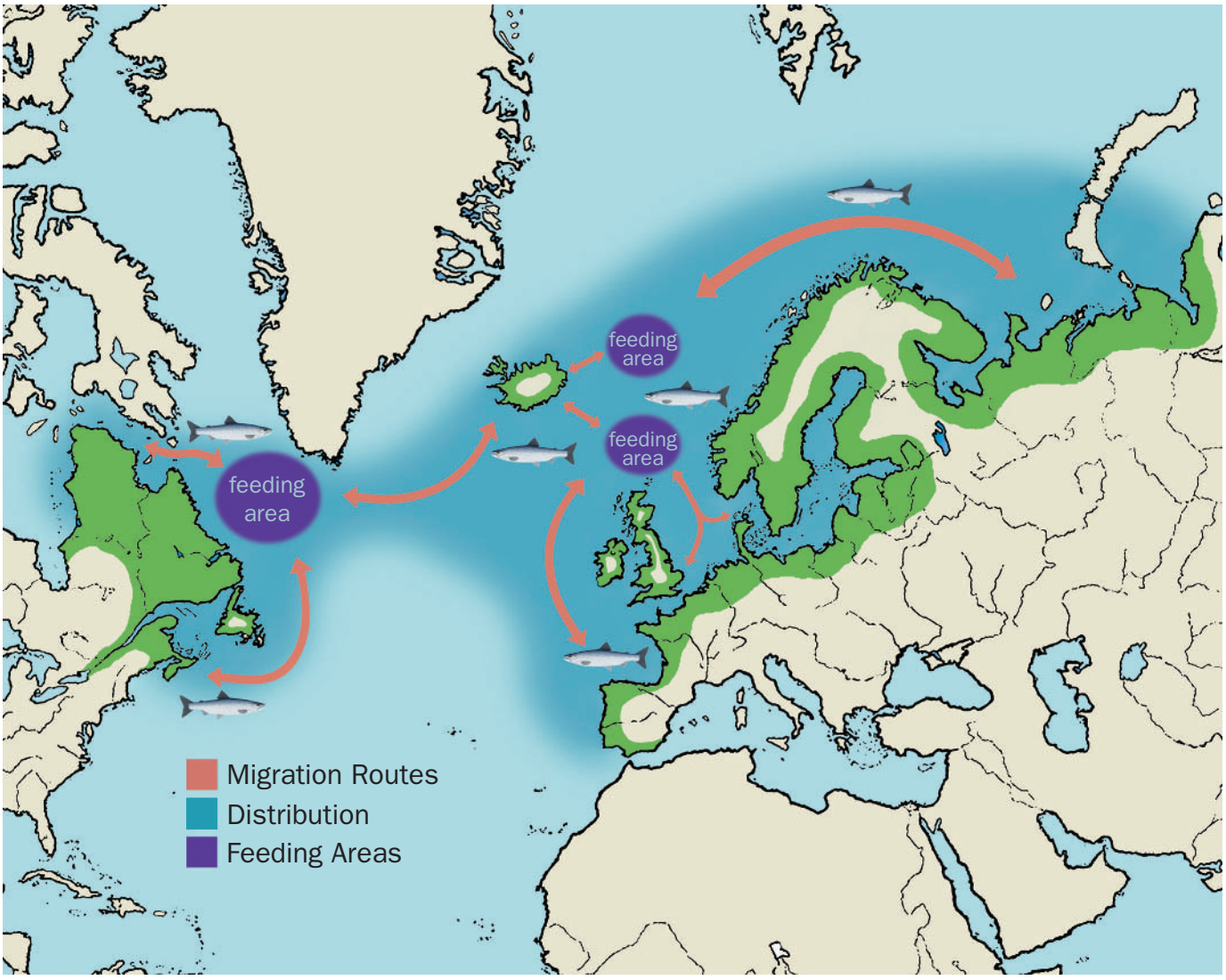
Distribution

Salmoniformes were originally found only in cool and cold waters of the Northern Hemisphere, where they are one of the most dominant freshwater fishes. In the North American continent, they are found from tributaries of the Arctic Ocean to tributaries of the Gulf of California in northwestern Mexico. They are also found from Eurasia to all Asia north to the Himalayas from the Arctic Circle south to Bangladesh, Manchuria, and the Korean Peninsula and the Japanese Islands and Taiwan. In Africa they are only found in the northwestern margin (Atlas mountains of Morocco and Algeria). The Arctic char (*Salvelinus alpinus*) is the world's most northerly occurring freshwater fish. Many species of this order have been successfully introduced in many other parts of the world.

Habitat

Many salmoniform species (such as trouts and salmons) have an anadromous life cycle, in that they spawn in fresh

Brook trout (*Salvelinus fontinalis*) in their vibrant autumn spawning colors. Note the tail of the male, lower left, showing a bite mark received during one of the many battles between males for the right to court a female. (Photograph. AP/Wide World Photos. Reproduced by permission.)



Salmon migration routes. (Illustration by John Megahan)

Grizzly bear fishing for salmon at a waterfall in Katmai National Park in Alaska. (Photo by Galen Rowell/Corbis. Reproduced by permission.)

waters, but migrate to sea for feeding and maturation. The pink salmon (*Oncorhynchus gorbuscha*) is the least anadromous species in the Pacific, since it has reduced the freshwater stage to the spawning migration and incubation of the eggs. Some individuals even spawn in the intertidal zone with no real freshwater phase. However, others are entirely freshwater, with completely landlocked local populations.

Behavior

Some species of Salmoniformes are fiercely territorial; others form schools shortly after hatching before they initiate their seaward migration. the most remarkable behavioral characteristic in these fishes is their strong swimming ability (some can leap over obstacles such as waterfalls as high as 10 ft/3 m) and their migratory capability. Almost all, if not all, Salmoniformes can return to the stream of their birth after migrating thousands of miles (or kilometers) in the ocean for one or more years, a behavior known as homing. They use their sense of smell to orient themselves, but some experi-

Sockeye salmon (*Oncorhynchus nerka*) spawning in North Fork Payette River, Idaho. (Photo by Willam H. Mullins/Photo Researchers, Inc. Reproduced by permission.)

ments suggest that vision and magnetic clues may also play a role in this behavior. This is not surprising, since other migratory species of animals, such as some birds, can use more than one source of information to achieve their migratory paths. Because of their migrations between fresh and salt waters, salmoniforms have developed a number of physiological adaptations to cope with changes in salinity. This is achieved via osmotic regulation by excreting excess salts through cells in the gills and by having well-developed kidneys, which, in fresh waters, excrete the excess water that diffuses into their blood via the gills.

Feeding ecology and diet

There is variation in feeding habits in this order. Some species feed upon plankton and benthic invertebrates, while others are top predators of other fish species.

Reproductive biology

All salmoniforms lay eggs that are externally fertilized. The egg size is related to the amount of nutrients in the water, with the largest eggs (0.16–0.31 in/4–8 mm), found in nutrient-poor waters. This allows individuals born under those conditions to have enough nutrients to survive, and is followed by direct development. This means that the young look very much like small adults. The size of the egg is also conversely proportional to the number of the eggs. In the case of smaller eggs, the young are less developed after hatching.

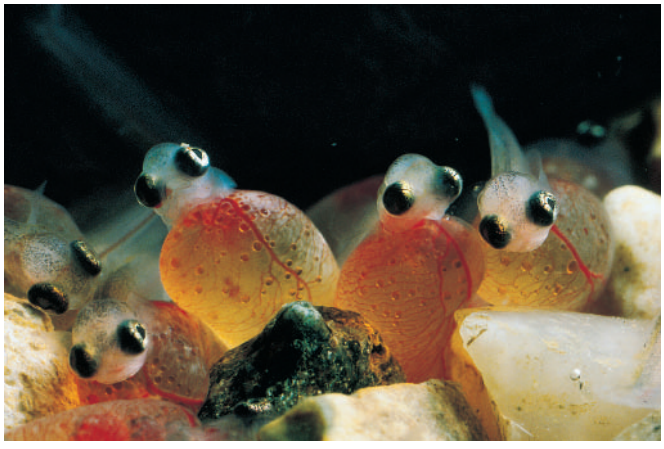
Conservation status

The IUCN Red List includes 36 salmoniform species. Of these, four are categorized as Extinct (*Coregonus alpenae*, *C. johannae*, *C. nigripinnis*, and *Salvelinus agassizi*); four are Critically Endangered; five are Endangered; 10 are Vulnerable; and 13 are Data Deficient.

Because all salmoniforms depend upon migrations into clear, highly oxygenated waters, they are very sensitive to water pollution as well as interruptions in the watercourse by means of dams. This problem is particularly acute for the Pacific salmon, whose numbers and genetic diversity have both declined dramatically.

Significance to humans

Many species of trouts, salmons, chars, whitefishes, and graylings are among the best-known and most intensively studied species of fishes. They have tremendous economic importance in many areas because of their value in both sport and commercial fisheries. This is the reason they have been introduced all over the world. Information about the life cycle and reproduction, some of it based on DNA analysis, has been used to settle disputes between nations regarding the origin of fishes caught in the open ocean, as well as for their management.



Close-up photo of newly hatched brown trout (*Salmo trutta*) on a river bed. (Photo by Science Pictures Ltd/Science Photo Library/Photo Researchers, Inc. Reproduced by permission.)

1. Brook trout (*Salvelinus fontinalis*); 2. Brown trout (*Salmo trutta*); 3. Lake trout (*Salvelinus namaycush*); 4. Charr (*Salvelinus alpinus*); 5. Atlantic salmon (*Salmo salar*); 6. Arctic grayling (*Thymallus arcticus arcticus*); 7. Lake whitefish (*Coregonus clupeaformis*). (Illustration by John Megahan)

1. Cherry salmon (*Oncorhynchus masou*); 2. Rainbow trout (*Oncorhynchus mykiss*); 3. Golden trout (*Oncorhynchus aguabonita*); 4. Chinook salmon (*Oncorhynchus tshawytscha*); 5. Pink salmon (*Oncorhynchus gorbuscha*); 6. Sockeye salmon (*Oncorhynchus nerka*); 7. Coho salmon (*Oncorhynchus kisutch*). (Illustration by John Megahan)

Species accounts

Lake whitefish
Coregonus clupeaformis

FAMILY
Salmonidae

TAXONOMY
Salmo clupeaformis Mitchill, 1818, Falls of St. Mary's River, Chippewa County, Michigan, United States. May be conspecific with *Coregonus lavaretus.*

OTHER COMMON NAMES
English: Common whitefish, eastern whitefish, lake whitefish; French: Grand corégone; German: Felchen; Spanish: Corégono; Inuktitut: Kavisilik.

PHYSICAL CHARACTERISTICS
Length 40 in (100 cm). A well-developed adipose fin, usually larger among males, characterizes this species. Coloration is dark brown to midnight blue above fading to silver on sides and white beneath.

DISTRIBUTION
North America throughout Alaska and most of Canada, south into New England, the Great Lakes basin, and central Minnesota. Successfully introduced in Chile and Argentina.

HABITAT
Primarily a lake dweller; can also be found in large rivers and enters brackish water.

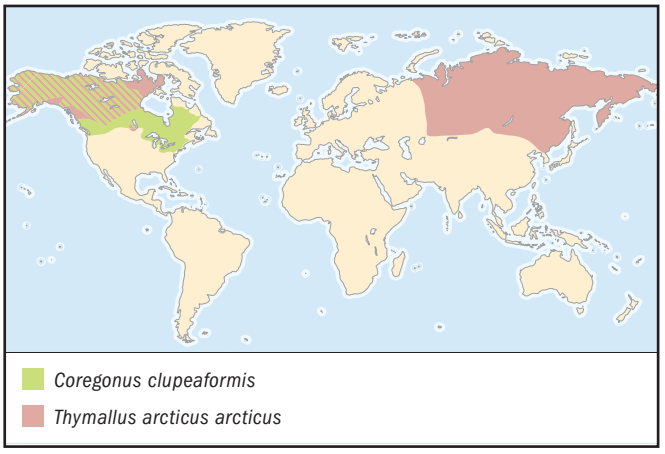
BEHAVIOR
When not migrating, tends to be sedentary in small lakes. Migration in large lakes consists of movement from deep to shallow water in the spring, movement back to deep water in the summer as the shoal water warms, migration to shallow-water spawning areas in the fall and early winter, and post-spawning movement back to deeper water.

FEEDING ECOLOGY AND DIET
Adults feed on aquatic insect larvae, amphipods, mollusks, as well as smaller fishes and fish eggs, including their own. They are vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Spawns annually at night from October through December. One female and one or more males rise to the surface where the eggs are released and fertilized. Spawning fish are very active, sometimes leaping out of the water. Eggs are demersal.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Extensively hatchery-reared in the Great Lakes and other areas because of their value as meat and roe. ◆



Golden trout
Oncorhynchus aguabonita

FAMILY
Salmonidae

TAXONOMY
Salmo mykiss aguabonita Jordan, 1892, Kern River California.

OTHER COMMON NAMES
French: Troite dorée; Spanish: Aguabonita.

PHYSICAL CHARACTERISTICS
Length 28 in (71 cm); maximum weight 11 lb (5 kg). One of the smallest species of trouts, characterized by a golden color with orange to red stripes along the side. In both the dorsal fin

and the area right before the tail, coloration is speckled with dark spots. This species is also known for its small scales.

DISTRIBUTION
High altitude, freshwater bodies in the western area of the United States, particularly in Wyoming, Idaho, Washington State, and most abundantly in California, where it was first discovered. Introduced in Canada.

HABITAT
Freshwater lakes and rivers at altitudes of 9,000–12,000 ft (2,740–3,700 m), generally in hard-to-access mountain areas. Because the waters they inhabit are very clear, with little vegetation, and of great beauty, the Spanish name is *aguabonita* (pretty water).

BEHAVIOR
Unlike other species of salmoniforms, largely a social species that travels in small schools. Active all summer. Because of their lack of aggressiveness and small size, they cannot compete with larger, more aggressive salmonids. This accounts for their restriction to headwaters of streams, where physical barriers such as waterfalls prevent other fish species from entering.

FEEDING ECOLOGY AND DIET
Diet includes surface water-dwelling insects, such as caddisflies and midges, as well as small crustaceans and terrestrial insects floating on the surface. Feeds mostly between May and September due to the scarcity of insects during winter. Practices a form of filter feeding, in which it opens the gills and inhales the prey whole, after which the food remains in the mouth. Vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
The development of this small species is rather brief when compared to that in other salmoniform species. The egg is almost completely ripe by the time temperatures arrest development at the beginning of winter. The fishes are then ready to spawn the following spring. The spawning routine begins at the time the snow starts to melt, sometime from March through July. As with other trout species, the female prepares the nest and lays her eggs in specific areas. After some behavioral displays, the males then come to fertilize them. Egg development, hatching, and early growth stages are virtually the same as in other spring spawners.

CONSERVATION STATUS
Translocated rainbow trouts aggressively out compete golden trouts and also hybridize with them. The *whitei* population has been classified as threatened since 1978 by the U.S. federal government. The California Department of Fish and Games Committee on Threatened Trout has been working to conserve and enhance the survival of this species. Although many attempts to stock this species in other appropriate waters in the western United States have taken place, most have not been successful.

SIGNIFICANCE TO HUMANS
Highly prized by sport fishers and much sought after as food. ◆

Pink salmon
Oncorhynchus gorbuscha

FAMILY
Salmonidae

TAXONOMY
Salmo gorbuscha Walbaum, 1792, rivers of Kamchatka, Russia.

OTHER COMMON NAMES
English: Humpback salmon; French: Saumon rose; German: Buckelkopflachs; Spanish: Salmón rosado.

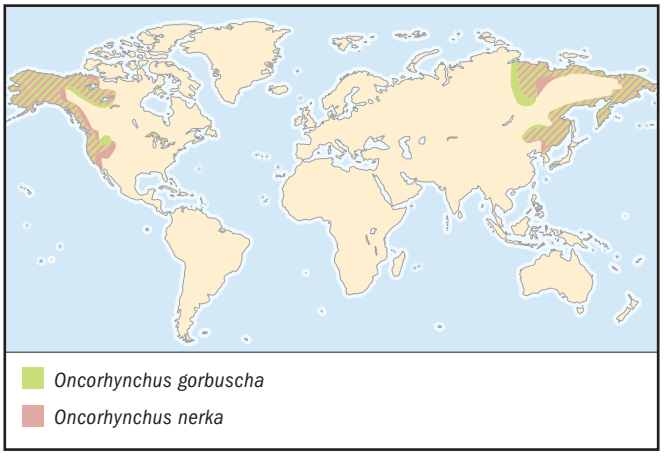
PHYSICAL CHARACTERISTICS
Length 30 in (76 cm); weight 15 lb (6.8 kg). The smallest of the true salmon species. Like most salmoniforms, has a streamlined, fusiform body, somewhat laterally compressed. The mouth is terminal, and among breeding males is greatly deformed by being very oblique, with the lower jaw enlarged and turned up at the tip, preventing the mouth from closing. Another characteristic is the presence of large black spots on the back and on both lobes of the caudal fin. The general coloration varies. Individuals at sea are steel blue to blue-green on the back, silver on the sides, and white on the belly, with large oval spots present on the back, the adipose fin, and on both lobes of the caudal fin. Breeding males are dark on the back, and red with brownish green blotches on the sides. Breeding females are similar to males, although less distinctly colored.

DISTRIBUTION
Arctic and Eastern Pacific, from eastern Korea and Hokkaido, Japan, to the Bering and Okhotsk Seas, to Alaska and the Aleutian Islands, to southern California, United States. Successfully introduced in Canada, Ireland, Norway, Greenland, Poland, Finland, and the United Kingdom.

HABITAT
Spends 18 months at sea before returning either to its native river or some other river to spawn. Unique because the homing behavior is not as strong as that of other salmoniform species. After emerging from the gravel, fry move downstream, remaining inshore for a few months before going out to sea.

BEHAVIOR
Reaches sexual maturity at two years of age. Both male and female die up to a few weeks after spawning.

FEEDING ECOLOGY AND DIET
The diet varies with age. Fry feed on nymphal and larval insects while in fresh water, but once at sea may not feed at all until they become juveniles, when they eat copepods and other zooplankton. As they continue to grow the food items shift toward larger crustaceans and fishes. They are preyed upon by other salmonids as fry, and by larger fishes (including sharks), fish-eating birds, and mammals as they grow.



REPRODUCTIVE BIOLOGY
Upstream migration takes place from June to late September, triggered by high water. The female builds the redd or spawning trench by lying on one side and using her tail to displace silt and light gravel. The accompanying male spends most of the time defending its territory. When the nest is complete, the female drops into it, followed immediately by the male. As for other salmoniforms, both male and female open their mouths, vibrate, and release eggs (1,200–1,800) and sperm. Then the eggs are covered by the female digging a new redd at the upstream edge of the previous one.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The flesh is highly prized; eggs are highly valued as caviar, particularly in Japan. ◆

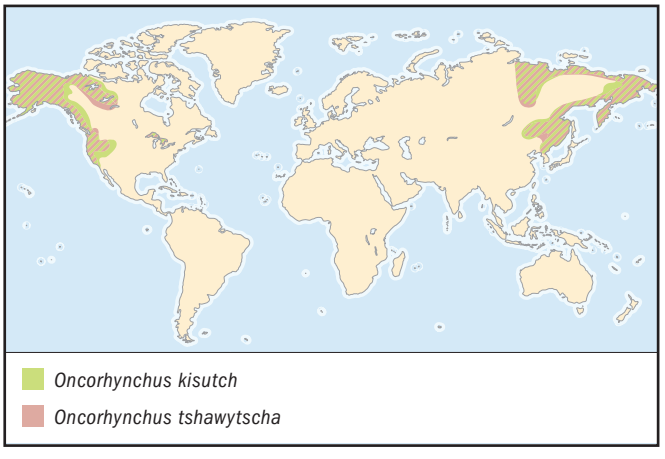
Coho salmon
Oncorhynchus kisutch

FAMILY
Salmonidae

TAXONOMY
Salmo kisatch Walbaum, 1792, rivers and lakes of Kamchatka, Russia.

OTHER COMMON NAMES
English: Blueback, silver salmon; French: Saumon argenté; German: Chumlachs; Spanish: Salmón plateado.

PHYSICAL CHARACTERISTICS
Length 42.5 in (108 cm) in males, 25.8 in (65.5 cm) in females; weight 35.5 lb (15.2 kg). Characterized by the presence of small black spots on the back and on the upper lobe of the caudal fin, as well as by the lack of dark pigment along the gum line of the lower jaw. Coloration varies according to environmental and reproductive conditions, as well as with sex. Females are generally more brightly colored than males. At sea all are dark metallic blue or greenish on the back and upper sides, with a brilliant silver color on middle and lower sides, and white below. In fresh water they display small black spots on the back and upper sides, and on upper lobe of the caudal fin. When ready for breeding they become dark to bright green on head and back and bright red on the sides, and often dark on the belly. The lateral line is nearly straight.



DISTRIBUTION
North Pacific in Asia from the Anadyr River in Russia in the north to Hokkaido, Japan, in the south. In North America from Point Hope in Alaska to Chamalu Bay, Baja California, Mexico. Successfully introduced in Chile, France, and the Laurentian Great Lakes in North America.

HABITAT
Oceans or lakes, returns to streams for spawning.

BEHAVIOR
Reach sexual maturity between two and four years of age.

FEEDING ECOLOGY AND DIET
Food items vary with age. Young in freshwater streams feed mainly on insects. Smolts feed on planktonic crustaceans upon reaching the sea. As they mature, they venture further into the ocean and feed on larger organisms. They are preyed upon by lampreys and various other species of fishes, birds, marine mammals, and bears.

REPRODUCTIVE BIOLOGY
Adults migrate from the sea or large lakes to the mouths of rivers, where they aggregate in large numbers forming schools. As rains increase the rivers' flow, they start swimming upstream. The reproductive behavior is very similar to that of the Chinook salmon. Females are in charge of finding the appropriate spot and digging a pit, they brush off any other female trying to do the same thing at the same spot. Attending males court females even while they are still digging the pit, As soon the pit is complete, the female drops into it, immediately followed by the male. After that, a ritualistic behavior takes place, which includes staying side by side and opening their mouths. This is followed by quivering and the release of eggs and sperm, with other males moving in and releasing sperm into the nest. The female then moves to the upstream edge of the nest and starts digging a new pit, covering the eggs. The entire process is repeated several times for several days, until the female deposits all her eggs and then dies. Meanwhile the male may pursue other females.

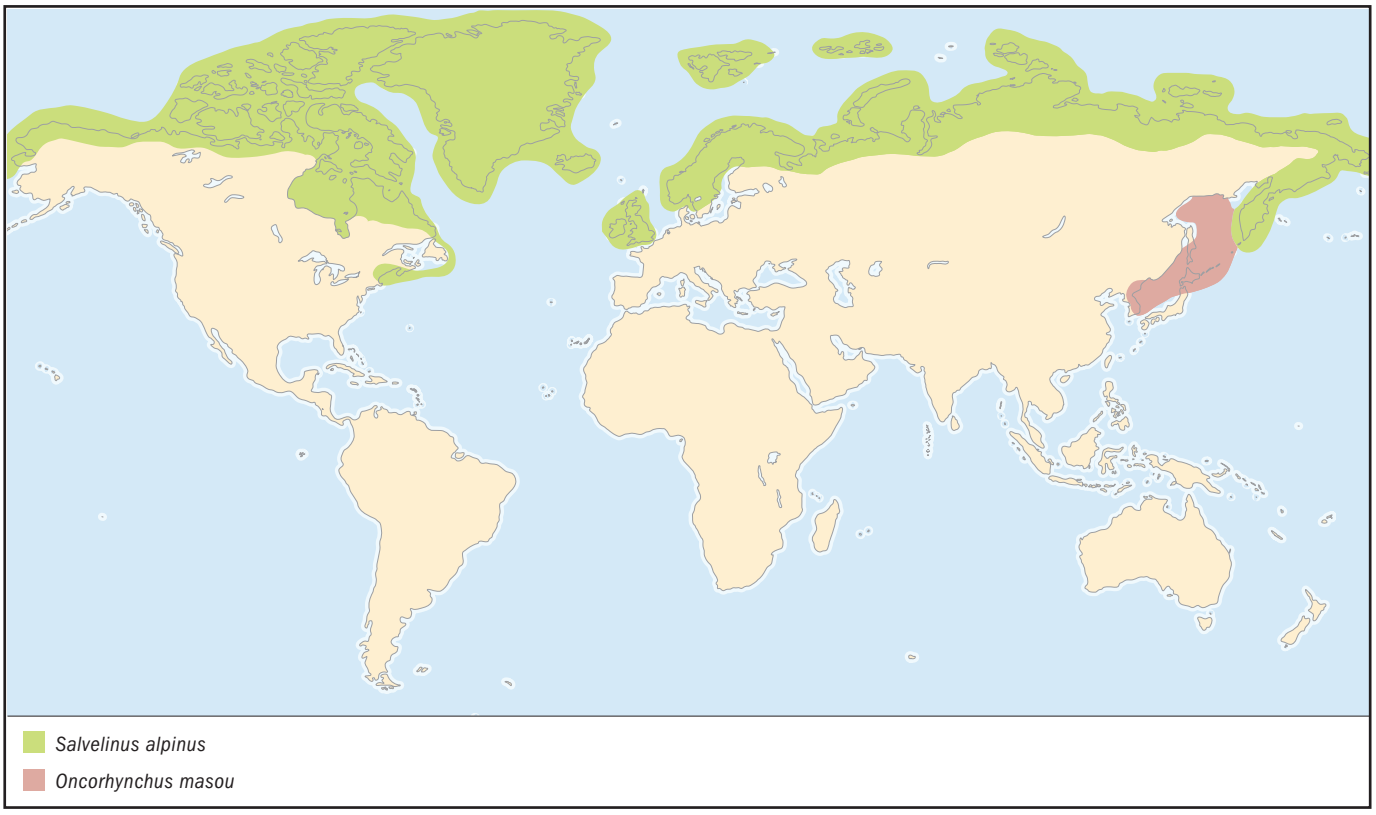
CONSERVATION STATUS
Not listed by the IUCN. The Alaskan fishery has been certified by the Marine Stewardship Council as well managed and sustainable.

SIGNIFICANCE TO HUMANS
Highly esteemed for its meat and supports important recreational fisheries in many parts of the world. ◆

Cherry salmon
Oncorhynchus masou

FAMILY
Salmonidae

TAXONOMY
Salmo masou Brevoort, 1856, Japan. There are two subspecies: one, *Oncorhynchus masou masou*, spawns in the sea; the other, restricted to freshwater, is yamame, or *Oncorhynchus masou ishikawae.*



OTHER COMMON NAMES
English: Salmon trout; French: Saumon masou; German: Masu-Lachs; Japanese: Masu.

PHYSICAL CHARACTERISTICS
Length 28 in (71 cm); weight 22 lb (10 kg). Troutlike shape. Coloration variable depending upon age and habitat or subspecies. Many adults have a general yellowish coloration and two series of gray oval spots: one fully laterally consisting of about 10 spots and one more dorsally consisting of five to six smaller spots. There are additional smaller spots over most of the rest of the body.

DISTRIBUTION
Northwest Pacific in Okhotsk Sea and Sea of Japan; northern Japan and eastern Korea Peninsula. Unlike other Pacific species of salmon, does not enter North American waters, and is said to be the most southerly salmonid. Introduced in Chile.

HABITAT
The river form generally inhabits headwaters.

BEHAVIOR
Like many other salmonids, defends a feeding territory.

FEEDING ECOLOGY AND DIET
Feeds mainly on insects and also on small crustaceans and fishes. The sea-run form goes downstream forming schools. After a short stay in the brackish zone it enters the sea, where it feeds on small fishes and pelagic crustaceans.

REPRODUCTIVE BIOLOGY
Not much is known about the reproduction of this species in nature, except that it is anadromous and spawns between August and October. Japanese hatcheries have promoted a number of programs designed to accelerate growth rate and fecundity by adding hormones to the diet.

CONSERVATION STATUS
Not listed by the IUCN. This species is monitored by The North Pacific Anadromous Fish Commission (NPAFC) established under the Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean, signed in 1992.

SIGNIFICANCE TO HUMANS
The common name derives from the Japanese nickname *sakurasmasu* (cherry salmon), a reference to the fact that it spawns at cherry blossom time. Marketed fresh and frozen; eaten broiled and baked. ◆

Rainbow trout
Oncorhynchus mykiss

FAMILY
Salmonidae

TAXONOMY
Salmo mykiss Walbaum, 1792, mouth of Columbia River at Fort Vancouver, Washington State, United States.

OTHER COMMON NAMES
English: Rainbow trout (North American landlocked populations), steelhead (sea populations); French: Truite arc-en-ciel; German: Regenbogenforelle; Spanish: Trucha arco iris.

PHYSICAL CHARACTERISTICS
Length 47.2 in (120 cm); weight 56 lb (25.4 kg). Body elongate and somewhat compressed, especially in larger individuals. Brightly colored, varies in color (especially males) depending upon habitat, size, and sexual condition. Stream residents and spawners are darker with more intense colors, lake residents tend to be lighter, brighter, and more silvery.

DISTRIBUTION
Eastern Pacific from Alaska to Baja California, Mexico. This is one of the most widely introduced fishes in the world in at least 50 countries, which makes its present distribution virtually global. In tropical countries where it has been introduced it is found only above 4,000 ft (about 1,200 m) of altitude above sea level. Introduction has had a negative ecological impact in many parts of the world.

HABITAT
Fresh waters where the water temperature is not higher than 53.6°F (12°C) in summer. Although they can be found in cold lakes, they require moderate-to-fast flowing, well-oxygenated waters for breeding. Yet, their survivorship is better in lakes than in streams.

BEHAVIOR
Adults aggressively defend feeding territories. All stocks of rainbow trout are opportunistic regarding migration, since they are able to migrate to, or at least to adapt to sea water, according to environmental factors. This may be another case of extreme behavioral plasticity.

FEEDING ECOLOGY AND DIET
Benthic feeders. Adults consume mostly aquatic and terrestrial insects, mollusks, crustaceans, fish eggs, minnows, and other small fishes (including other trouts). Young feed mostly on zooplankton. Ocean-going populations are vulnerable to larger fishes, pinnipeds, and toothed whales. Freshwater populations are preyed upon by larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
As for other salmonids, growth rate varies according to environmental conditions. Usually reach sexual maturity between two and three years of age, with some extreme cases becoming sexually mature at five years. In this species, the female finds a spot and digs a pit. However, while she digs she is accompanied by an attendant male, which courts her and also drives away other males. Once the pit is completed, the female drops into it, immediately followed by the male. When the pair is side by side, they open their mouths, quiver, and release egg and sperm. A total of 700–4,000 eggs are produced per spawning event, which are then fertilized by the subordinate male. The female then quickly moves to the upstream edge of the nest and starts digging a new pit, covering the eggs. This process goes on for several days until the female has deposited all her eggs. The young move downstream at night, shortly after they emerge.

CONSERVATION STATUS
Not listed by the IUCN. However, in May 2002 the National Marine Fisheries Service (under the Endangered Species Act) issued a ruling redefining the geographic range of the listed anadromous population of this species to include all steelheads and their progeny occurring in coastal river basins from the Santa Maria River (inclusive) to the United States/Mexico Border. Within the redefined geographic range, only anadromous, naturally spawned populations and their progeny, which reside below naturally occurring and man-made impassable barriers, such as impassable waterfalls and dams, are listed as endangered.

SIGNIFICANCE TO HUMANS
Perhaps the most often bred fish species in the world because of its adaptability and value as the subject of commercial and sports fisheries. Anglers find it very interesting because of its spectacular leaps and hard fighting when hooked. ◆

Sockeye salmon
Oncorhynchus nerka

FAMILY
Salmonidae

TAXONOMY
Salmo nerka Walbaum, 1792, rivers and seas of Kamchatka, Russia.

OTHER COMMON NAMES
English: Blueback salmon, land-locked sockeye, red salmon; French: Saumon rouge; German: Blaurücken; Spanish: Salmon rojo.

PHYSICAL CHARACTERISTICS
Length 33 in (84 cm) in males, 28 in (71 cm) in females; weight 17 lb (7.7 kg). Like most salmoniforms, has a streamlined, fusiform body that is laterally compressed, but unlike other species, the body depth is moderate, slightly deeper among breeding males. Head is conical, very pointed, with small eyes. Lateral line is straight. Has long, fine, serrated, and closely spaced gill rakers on the first arch. Coloration varies with sex and reproductive stage. Pre-spawning individuals are dark steel blue to greenish blue on the head and back, silvery on the sides, and white to silvery on the belly. Spawning individuals (particularly males) have a bright to olive green head with black on the snout and upper jaw; the adipose and anal fins turn red and the paired fins and tail generally become grayish to green or dark. Females are less brightly colored than males.

DISTRIBUTION
North Pacific, from northern Japan to Bering Sea and to Los Angeles, California, United States, with landlocked populations in Alaska, Yukon Territory, and British Columbia in Canada, and Washington and Oregon, United States. Successfully introduced in New Zealand.

HABITAT
There are two forms of this species: the sockeye, an anadromous form (a marine form that migrates to fresh water for spawning), and the kokanee, a landlocked form (with a much smaller maximum size).

BEHAVIOR
Age structure and morphology differ among populations. Sexual selection and reproductive capacity (fecundity and egg size) generally favor large (old), deep-bodied fish, thus the sizes and shapes of salmon vary among spawning habitats. Stream width is positively correlated with age at maturity and negatively correlated with the level of predation by bears. Therefore, sexual maturity can be reached as early as at one year of age or as late as five. Adults show a great inclination for homing, which takes place during summer and fall, as late as December.

FEEDING ECOLOGY AND DIET
Young in lakes feed largely on crustaceans and insect larvae; adults in lakes become pelagic and feed on plankton in the upper 60 ft (20 m) or so of the water column. As they grow, their diet starts to include other fishes. The landlocked form feeds

mainly on plankton, insects, and benthic organisms. Ocean-going populations are preyed upon by larger fishes, including sharks, as well as by pinnipeds and killer whales. Freshwater populations are vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Like other salmoniforms, the female selects a site to dig a nest, where she is attended by a dominant male along with a few subordinate males. Both females and males protect their site by aggressively shoving off individuals of the same sex. After courtship by the dominant male, the female enters the nest, followed immediately by the dominant male, which comes close beside her. After the ritual of mouth gaping, the pair vibrates to release eggs and sperm, and one or more subordinate males comes to the other side of the female and joins in the spawning. The female then moves to the upstream edge of the nest and digs again, covering the old nest, while at the same time creating a new one just upstream. After three to five days of depositing eggs, the female is exhausted and, along with the male, dies. The fry emerging from the gravel is very photophobic, and becomes mostly nocturnal.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
One of the most commercially important Pacific salmons. The kokanee form is much sought after as a sport fish and is valued as food. ◆

Chinook salmon

Oncorhynchus tshawytscha

FAMILY
Salmonidae

TAXONOMY
Salmo tshawytscha Walbaum, 1792, rivers of Kamchatka, Russia.

OTHER COMMON NAMES
English: King salmon, Pacific salmon; French: Saumon chinook; German: Königslachs; Spanish: Salmón chinook.

PHYSICAL CHARACTERISTICS
Length 59 in (150 cm); weight 136.36 lb (61.4 kg). The fusiform body is streamlined and laterally compressed among large adults. Important distinguishing characteristics are small black spots on the back and the upper and lower lobes of the caudal fin, as well as on the black gums of the lower jaw. The gill rakers are widely spaced and rough. Coloration varies with environmental conditions. At sea, adults are dark greenish to blue black on top of head and back and silvery to white on the lower sides and belly; they also present numerous small and dark spots along back and upper sides and on both lobes of the caudal fin. In fresh water, they acquire an olive brown to red or purplish coloration, which is particularly noticeable among males.

DISTRIBUTION
Arctic and Pacific regions, in the drainages from Point Hope, Alaska to California, United States, as well as Japan, the Bering Sea, and the Okhotsk Sea. Successfully introduced in Australia, New Zealand, and Chile.

HABITAT
Similar to that of other salmoniforms; however, in lakes they may inhabit depths down to 1,230 ft (375 m).

BEHAVIOR
Like other salmoniforms, adults show a strong homing behavior. Their migratory behavior varies greatly. Usually, after three months in fresh water, most fry migrate to the sea, although some may stay in fresh waters for as long as three years. Some individuals remain close inshore throughout their lives, others make extensive migrations.

FEEDING ECOLOGY AND DIET
Food in streams consists mainly of terrestrial insects and small crustaceans; at sea major food items include fishes, crustaceans, and other invertebrates. The young are preyed upon by fishes and birds, such as mergansers and kingfishers; adults are preyed upon by sharks, large mammals (including killer whales), and birds.

REPRODUCTIVE BIOLOGY
Anadromous adults can migrate nearly 3,100 mi (5,000 km) from the ocean upstream to spawn. In December adults start to migrate from the sea, so that by early spring the first individuals arrive near the river mouths. The female is in charge of selecting the spawning spot where she will dig her nest, and aggressively drives away other females competing for the same spot. Once she has established her territory, a dominant male and several smaller males join her, at the same time driving away other males that compete for her. Male courtship behavior includes resting beside the female, quivering, swimming around over her, touching her dorsal fin with his body and fins, and occasionally nudging her side gently with the snout. Once the nest is complete, the female drops into it, and is immediately joined by the dominant male. Both open their mouths, vibrate, and eggs and sperm are released. At this point smaller males may swim into the nest and release their own sperm. (It is unclear to what extent these smaller males play a role in fertilizing the eggs.) The female then quickly covers the eggs by moving to the upstream edge of the nest and digging small pebbles for a new nest. This process, which may last several days, is repeated several times, until the female releases all her eggs. The female guards the nest for as long as she can. The male leaves the female and may mate with another female. Spent adults usually die a few days after spawning.

CONSERVATION STATUS
Not listed by the IUCN. The Alaskan fishery of this species has been certified by the Marine Stewardship Council as well managed and sustainable.

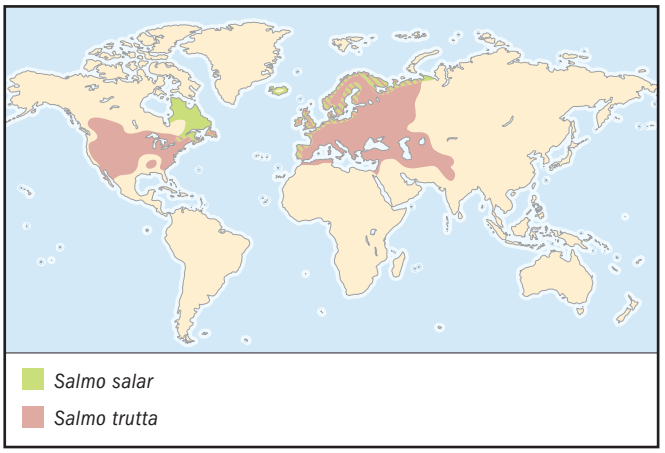
SIGNIFICANCE TO HUMANS
Highly regarded commercial and game fishes, whose red meat commands a high price. The viscera are rich in vitamin A and are used as food for hatchery fish. ◆

Atlantic salmon

Salmo salar

FAMILY
Salmonidae

TAXONOMY
Salmo salar Linnaeus, 1758, "Seas of Europe."



OTHER COMMON NAMES
English: Black salmon, sea salmon; French: Saumon Atlantique; German: Atlantischer Salmon; Spanish: Salmón.

PHYSICAL CHARACTERISTICS
Length in males 59.1 in (150 cm), in females 47.2 in (120 cm); weight 103 lb (46.8 kg). Individuals display different morphology and coloration depending upon the phase of the breeding season or the habitat they are in. Body usually has black spots, caudal fin usually is unspotted, and adipose fin is not black bordered. Other times they are blue-green overlaid with a silvery guanine coating in salt water, losing silvery coat to become greenish or reddish brown mottled with red or orange in freshwater.

DISTRIBUTION
Western Atlantic in the coastal drainages from northern Quebec, Canada, to Connecticut, United States; Eastern Atlantic in drainages from Arctic Circle to Portugal. Some landlocked stocks can be found in North America, Norway, Finland, Sweden, and Russia. Successfully introduced in Chile, Argentina, Finland, Australia, and New Zealand.

HABITAT
Juveniles inhabit freshwater; adults inhabit marine waters except to spawn. Usually found in rocky runs and pools of rivers, large and small, as well as lakes.

BEHAVIOR
Young remain in freshwater for one to six years, after which they migrate to the ocean. They remain there for one to four years, before returning to fresh water to spawn, then they return to the sea. Active mostly during the day.

FEEDING ECOLOGY AND DIET
Juveniles feed on mollusks, crustaceans, insects, and fishes; adults at sea feed on squids, shrimps, and fishes. Ocean-going populations are vulnerable to larger fishes, pinnipeds, and toothed whales. Freshwater populations are preyed upon by larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Growth rate depends on food availability and quality, as well as on water temperature and photoperiods. They reach sexual maturity between three and seven years of age. Adults reaching sexual maturity return to their home rivers, usually to the same areas where they were hatched and spent their initial freshwater life. Once there, the female selects a spawning site with appreciable current based on depth (usually 1.6–9.6 ft (0.5–3 m) and gravel size. Then she excavates a hole by turning on her side and flexing her body up and down creating a current and never touching the stones. After the female releases 8,000–26,000 eggs, the males visit the area, fertilize them, and cover the eggs. Spawning takes between two and three days. Early maturing or sneaker males return to their home stream every year, older males do so after several years in the ocean. The older males are not only larger, but also more colorful. Aggregations around a female are composed of both sneaker (smaller, younger) and older males. Once the female releases her eggs, all males release their sperm, with the greater number of eggs being fertilized by the first male that enters the nest. Young salmons fathered by precocious males grow faster than those fathered by anadromous males. Juvenile salmons (known as parr) spend most of their freshwater life in shallow riffles, mostly at the southern end of their range, until they reach 4–5 in (12–15 cm) in length, when they transform themselves into smolt and are ready for migration in spring the first year after hatching.

CONSERVATION STATUS
Not listed by the IUCN. Listed in Appendix III of The (Bern) Convention on the Conservation of European Wildlife and Natural Habitats as long as the species is in fresh waters.

SIGNIFICANCE TO HUMANS
Commercially valued for meat and consumed in many forms. ◆

Brown trout
Salmo trutta

FAMILY
Salmonidae

TAXONOMY
Salmo trutta Linnaeus, 1758, "Europe."

OTHER COMMON NAMES
English: German brown trout, herling, sea trout; French: Truite brune de mer; German: Lassföhren; Spanish: Trucha común.

PHYSICAL CHARACTERISTICS
Length 55.1 in (140 cm); weight 110.4 lb (50 kg). Coloration varies only according to the breeding season. They are dorsally black, usually orange on sides, surrounded by pale halos. The adipose fin has always a red margin. Troutlike body. The upper jaw reaches below the center of the eye in juveniles and well beyond the eye in larger individuals.

DISTRIBUTION
Originally from Eurasia. Now introduced all over the world, including Europe, Latin America, Australia, and New Zealand. Widely transplanted because it thrives in warmer waters than most other species of trouts. As with other species of salmonids, the introductions have had a negative impact on the local fauna.

HABITAT
Prefers cold, well-oxygenated upland waters. Favorite habitat is large streams in mountain areas with submerged rocks, undercut banks, and overhanging vegetation. Preferences in terms of high temperature tend to be looser than that of the rainbow trout.

BEHAVIOR
Mainly diurnal. Very territorial, aggressively defends feeding areas from conspecifics (members of the same species) and other trout species.

FEEDING ECOLOGY AND DIET
Diverse diet including small aquatic and terrestrial insects, mollusks, crustaceans, and small fishes. When eating very small prey, utilizes gill rakers on the surface of the gill arches. The plasticity in feeding preferences is accompanied by morphological plasticity in the feeding apparatus. For example, the mouth is fairly large and has nonspecialized teeth on the jaws and on several bones within the mouth, which serve for eating any almost creature. Very voracious, adults prey on items up to one-fourth their own length. The well-defined muscular stomach opens by a valve into the intestine. The intestine has a series of fingerlike appendages (pyloric ceca) that open off the intestine, immediately posterior to the stomach. These appendages secrete enzymes to facilitate food digestion. This character is typical of many very predacious species, and the more predacious they are, the higher the number of pyloric ceca. Ocean-going populations are vulnerable to larger fishes, pinnipeds, and toothed whales. Freshwater populations are preyed upon by larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Life history is similar to that of the Atlantic salmon, reproducing in rivers, producing about 10,000 eggs, and taking between three and four years for maturation.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Much sought after as a food item, particularly in Europe. Ocean-going individuals are called sea trout, and are larger than freshwater forms. They provide good sport, as do those that enter large lakes. ◆

Charr
Salvelinus alpinus

FAMILY
Salmonidae

TAXONOMY
Salmo alpinus Linnaeus, 1758, "Europe."

OTHER COMMON NAMES
English: Alpine char, Arctic charr; French: Omble arctique; German: Schwarzreuter; Spanish: Trucha alpina; Inuktitut: Akalukpik; Italian: Salmerino alpino; Portuguese: Truta-das-fontes.

PHYSICAL CHARACTERISTICS
Length 42 in (107 cm); weight 33 lb (15 kg). Distinguished from other species by light rather than black spots and by a boat-shaped bone (vomer) that is toothed only in front, on the roof of the mouth. Another distinguishing characteristic is the presence of 23–32 gill rakers and pink to red spots on the sides and back, the largest of which are usually larger than the pupil of the eye. Unlike other salmoniforms, the lateral line is not straight, but curves slightly downward from the head. Coloration varies with location, time of year, and degree of sexual development. Generally the back is dark, mostly brown, but also somewhat green, with lighter sides and a rather pale belly. Spawning adults, especially males, acquire very bright orange to red coloration on the ventral side and on the pectoral, pelvic, and anal fins.

DISTRIBUTION
North America and Europe in the Arctic and adjacent oceans, also rivers and lakes they enter to breed. This distribution includes the North Atlantic south to southern Norway, including Iceland and southern Greenland. There are isolated populations in northern United Kingdom, Scandinavia, Finland, and the Alps. Other populations are restricted to freshwater lakes (colonized in glacial times) in Quebec, Canada, and in Maine and New Hampshire, United States. Successfully introduced in Yugoslavia and France.

HABITAT
Like other salmoniforms this is an anadromous species found in fresh, brackish; and marine waters ranging in depth from 100 to 230 ft (30–70 m).

BEHAVIOR
Little is known besides feeding and reproductive behavior.

FEEDING ECOLOGY AND DIET
Freshwater populations feed on planktonic crustaceans, amphipods, mollusks, insects, and fishes (particularly finfish). Large individuals are piscivorous; dwarf and small fishes feed on a wide range of invertebrates. The proportion of plankton in the diet of dwarf and small individuals correlates positively with the number and length of gill rakers. Ocean-going populations are preyed upon by larger fishes and pinnipeds. Freshwater populations are vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Males reach sexual maturity between 4 and 5 years of age, females do so between 5 and 10 years old. The males establish a territory in order to attract females. When the female enters the territory, she looks for a suitable spot for a redd (nest) and starts digging. As she does, the male begins its courting behavior by circling around her and then gliding along her side and quivering. Once the redd is complete, the pair release egg and sperm. The female then covers the eggs by digging at the edge of the pit, thus starting the next redd. In the subarctic Lake Fjellfrosvatn, northern Norway, there are two morphs of Arctic charr that are reproductively isolated because they spawn five months apart. The smaller morph (less than or equal to 5.5 in [14 cm]) is confined to the deeper zones of the lake, the larger morph is mainly littoral.

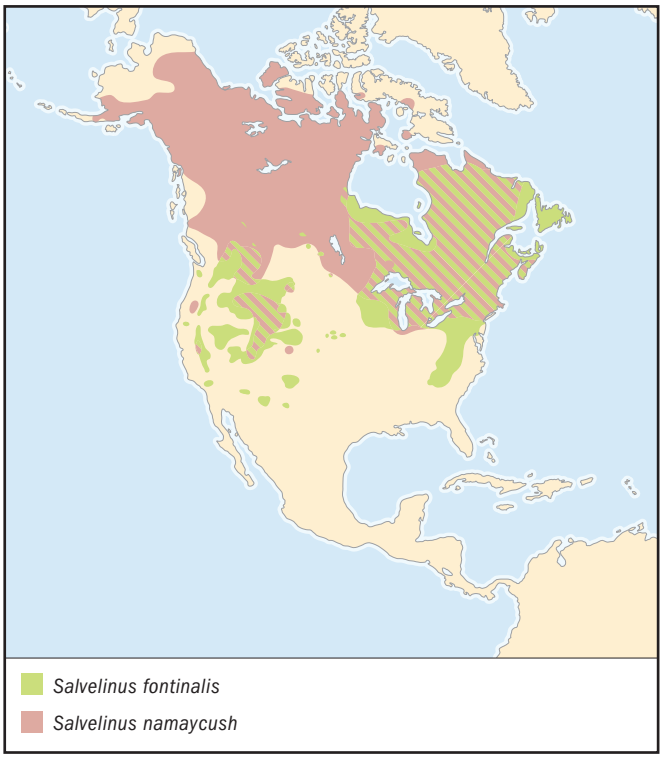
CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Highly prized as both a food and sport fish. ◆

Brook trout
Salvelinus fontinalis

FAMILY
Salmonidae

TAXONOMY
Salmo fontinalis Mitchill, 1814, vicinity of New York City, New York, United States.



OTHER COMMON NAMES
English: Brook charr, speckled trout, squaretail; French: Omble de fontaine; German: Bachsaibling; Spanish: Salvelino; Inuktitut: Iqaluk tasirsiutik.

PHYSICAL CHARACTERISTICS
Length 33.9 in (86.0 cm); maximum weight 20.7 lb (9.39 kg). Characterized by combination of dark green marbling on the back and dorsal fin, and by red spots with blue halos on the sides. Coloration can vary among populations and in reproductive states, with lower sides and fins red in spawning fishes. While migrating, dark green above with silvery sides, and white bellies and pink spots.

DISTRIBUTION
North America in most of eastern Canada from Newfoundland to western side of Hudson Bay; south in Atlantic, Great Lakes, and Mississippi River basins to Minnesota and northern Georgia, United States. In general, south of the Hudson River, distribution is correlated to altitude. For example, populations in North Carolina and Georgia are restricted to headwaters of streams in the Piedmont region of the Appalachians. Introduced in temperate regions all over the world.

HABITAT
Clear, cool, well-oxygenated creeks, small to medium rivers, and lakes.

BEHAVIOR
Migrates upstream in early spring, summer and late fall, migrates downstream in late spring and fall. As stream temperatures rise in the spring, may run to the sea (never more than a few miles [kilometers] from river mouths) and stay there for up to three months.

FEEDING ECOLOGY AND DIET
Opportunistic feeders, eating worms, leeches, crustaceans, insects, mollusks, fishes, amphibians, and even small mammals and plant matter. Littoral individuals exhibit lower physiological performance than do pelagic individuals, when restricted to feeding in the pelagic zones. Ocean-going populations are preyed upon by larger fishes and pinnipeds. Freshwater populations are vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Reaches sexual maturity between one and three years, with variable growth rates depending upon temperature conditions. Spawning takes place from October through December. Hatching takes about 100 days or longer if waters are below 41°F (5°C). The male courts females by attempting to drive them toward a suitable spawning gravel site that he will defend aggressively. If a female is receptive, she will choose a spot and dig a redd. Even while the female is digging, the male continues its courtship by darting alongside the female, swimming over and under her, and rubbing her with his fins. When the redd is complete, the pair enter the nest and deposit eggs and milt (sperm). The female then covers the eggs with small pebbles. Once the eggs are completely covered, she moves to the upstream end of the redd and begins digging a new redd. Early maturing, dwarf "jack" or sneaker males return to their home stream every year; "hooknose" males do so after several years in the ocean. The latter are not only larger, but also more colorful. Aggregations surrounding a female are composed of both "jacks" and "hooknose" males. Once the female releases her eggs, all males release their sperm, with the greater number of eggs being fertilized by the first male that enters the nest. Individuals of this species can reach 15 years of age in captivity.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Commercially farmed because of their value as food, also used extensively as an experimental animal. Anglers regard them highly because of their fighting qualities when hooked. ◆

Lake trout
Salvelinus namaycush

FAMILY
Salmonidae

TAXONOMY
Salmo namaycush Walbaum, 1792, Hudson Bay.

OTHER COMMON NAMES
English: Great Lake trout, lake charr, Mackinaw trout, salmon trout; French: Omble d'Amérique; German: Amerikanische Seeforelle; Spanish: Trucha lacustre; Inuktitut: Isuuq.

PHYSICAL CHARACTERISTICS
Average length 59 in (150 cm); average weight 72 lb (32.7 kg). Body typically troutlike, elongate, somewhat rounded, with a stout head that is dorsally broad. The deeply forked tail distinguishes them from other species. The lateral line is slightly curved at the front. Coloration characterized by white or yellowish spots on a dark green to grayish background, but also have pale spots on dorsal, adipose, and caudal fins, and usually on base of anal fin; sometimes orange-red on paired fins. During spawning males develop a dark lateral stripe and become paler on the back.

DISTRIBUTION
North America, from northern Canada and Alaska, south to New England in United States, and Great Lakes basin in Canada and the United States. Successfully introduced in many other areas, including South America, Europe, and New Zealand.

HABITAT
Shallow and deep waters of northern lakes and streams, rarely brackish waters.

BEHAVIOR
Sexually mature fishes return to the rocky creek where they were spawned in the same manner that river-living salmonids return home to their natal stream.

FEEDING ECOLOGY AND DIET
Extremely voracious. Most populations feed on freshwater sponges, crustaceans, insects, fishes, and small mammals; others feed on plankton throughout their lives. Planktivorous trouts show characteristics typical of plastic (variable) populations. For example, they grow more slowly, mature earlier and at smaller size, die sooner, and attain smaller maximum size than do their fish-eating counterparts. Vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
More or less dispersed away from the spawning beds during the day, returning in late afternoon and spawning mostly at night, particularly between dusk and 9 or 10 P.M. Males establish their territory by rocks on the substrate, females arrive a few days later when males court them. From one to seven males will approach one to three females in the same area and press themselves against the sides of one or more females. Then the eggs fall into the crevices and the spawners disperse. This behavior is repeated until the female releases all her eggs. The eggs are heavy and sink to the bottom.

CONSERVATION STATUS
Not listed by the IUCN, yet they are highly susceptible to insecticides. In the 1930s sea lampreys invading the Great Lakes reduced this species almost to extinction. Great Lakes populations are largely sustained by extensive stocking of hatchery-reared fry.

SIGNIFICANCE TO HUMANS
Fished by both commercial and sport fishers. ◆

Arctic grayling
Thymallus arcticus arcticus

FAMILY
Salmonidae

TAXONOMY
Salmo arcticus Pallas, 1776, Ob River, Siberia, Russia.

OTHER COMMON NAMES
English: American grayling, Black's grayling; French: Ombre arctique; Russian: Kharius sibirskiy; Inuktitut: Sulukpauga.

PHYSICAL CHARACTERISTICS
Length 30 in (76.0 cm); weight 8.45 lb (3,830 g). They have a dark, enlarged dorsal fin (especially among males) and a small mouth with fine teeth on both jaws. The pelvic fins are rather long, reaching the anal fin in adult males, but not in females. The lower lobe of caudal fin is usually longer than the upper. Bodies are brightly colored, dark purple or blue-black to blue-gray in dorsal areas; sides are gray to dark blue with pinkish iridescence, gray to white in ventral region. Scattered dark spots on sides, particularly the young, with a dark longitudinal stripe along lower sides between pectoral and pelvic fins.

DISTRIBUTION
North America in the Arctic drainages from Hudson Bay, Canada to Alaska, and in Arctic and Pacific drainages to central Alberta and British Columbia in Canada. Relict populations are also found in the upper Missouri River drainage in Montana, United States. Past distribution included the Great Lakes basin in Michigan, United States, and in Siberia, Russia.

HABITAT
Clear, open waters of cold, medium-to-large rivers and lakes. Spawns in rocky creeks.

BEHAVIOR
Forms schools of moderate numbers.

FEEDING ECOLOGY AND DIET
Young feed on zooplankton but later prefer immature insects. Adults feed mainly on surface insects as well as other fishes, fish eggs, lemmings, and planktonic crustaceans. Vulnerable to larger fishes, otters, bears, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Sexual maturity comes between two and six years of age. Spawning takes place between April and June. Once spawning adults move into tributaries, males establish territories. When a female enters a territory, males court her with displays of the dorsal fin. Then he positions himself beside the female and curves his extended dorsal fin over her. The pair releases eggs and milt while vibrating, with that vibration stirring up the substrate to produce a slight depression. After spawning, adults establish summer territories in pools farther upstream from the spawning site, returning downstream in mid-September.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Utilized as food and as an object of recreational fishery.

Resources

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Organizations

Salmon and Trout Association (UK). Fishmongers' Hall, London Bridge, London, EC4R 9EL UK. Phone: (020) 7283 5838. Fax: (020) 7626 5137. E-mail: salmon.trout@virgin.net Web site: http://www.salmon-trout.org

United States Trout Farmers Association. 111 West Washington St., Suite One, Charles Town, WV 25414-1529 USA. Phone: (304) 728 2189. Fax: (304) 728 2196. E-mail: ustfa@intrepid.net Web site: http://www.ustfa.org

Other

The Northwest Salmon Crisis: A Documentary History [cited January 29, 2003]. <http://www.netLibrary.com/urlapi.asp?action=summary>

"Pictures available for *Oncorhynchus masou*" [cited February 7, 2003]. <http://www.fishbase.org/Photos/ThumbnailsSummary.cfm?ID=242>

"*Oncorhynchus masou masou*" [cited February 7, 2003]. <http://www.city.chitose.hokkaido.jp/tourist/salmon/event/miniatrure/masou.html>

Stomiiformes
(Dragonfishes and relatives)

Class Actinopterygii
Order Stomiiformes
Number of families 4

Photo: The sabertooth viperfish (*Chauliodus sloani*) lives in the deep sea. (Photo by Dr. Paul A. Zahl/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The fossil record of the stomiiform fishes is scant, as is the case with most groups of thin-boned deep-sea pelagic fishes. The oldest known stomiiform-like fossils (*Paravinciguerria*) date back to the Upper Cretaceous, some 70 million years ago, though critical evaluation has shed some doubt as to whether it is related. Fossil evidence suggests that the hatchetfish family Sternoptychidae arose during the early Tertiary and reached its present evolutionary grade by the mid-Miocene, 16 million years ago. Several other fossils from the Miocene have been placed in modern stomiiform genera. In general, the fossils that have been described and verified as stomiiform-like differed little from recent forms. As such, they have not proven highly useful in determining the origin of stomiiform fishes. In a 1984 treatise on the origin of pelagic fishes, Nikolay Parin suggested that the Stomiiformes, an order of entirely pelagic, open-ocean fishes, arose from fishes living near the bottom of the deep sea. In *Interrelationships of Higher Euteleostean Fishes*, published in 1973, Donn Rosen stated that the ancestral form of the Stomiiformes is thought to be allied with the salmon-like fishes.

Among living fishes, the Stomiiformes are thought to be most closely related to the "jellynose fishes" of the order Ateleopodiformes. (Ateleopodiformes is a closely related order that has not been resolved completely [Olney et al. 1993], and is not discussed here.) These two orders comprise the Stenopterygii, which is the basal taxon of the Neoteleostei ("new bony fishes"). With respect to the entire spectrum of fishes, the stomiiforms can be thought of as more advanced than eels, herrings, minnows, catfishes, and trout, but more primitive than lanternfishes, cod, bass, and flounders.

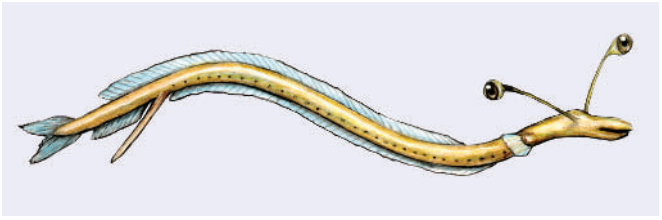
Currently, four families are recognized: Gonostomatidae (bristlemouths), Phosichthyidae (lightfishes), Sternoptychidae (marine hatchetfishes), and Stomiidae (dragonfishes and relatives). The classification of families within this order was radically revised in 1985. At that time William Fink combined the 230 or so species of "barbeled stomiiforms," previously recognized in six families, into one large family, the Stomiidae. At the close of the twentieth century, approximately 321 species of stomiiform fishes were described, grouped in two suborders, four families, nine subfamilies, and 51 genera. The majority of the species occur within the Stomiidae, and almost half of these species belong to a single dragonfish genus, *Eustomias*.

Physical characteristics

The stomiiform fishes are small to moderate in size, ranging from 0.6 in (15 mm) to 20 in (508 mm). The high species diversity of the Stomiiformes is matched only by its morphological diversity. Some species are extremely elongate and slender, while others are deep-bodied and laterally compressed. In one group there are radical differences in the form of males and females (called sexual dimorphism; see *Idiacanthus fasciola* species account). The order Stomiiformes includes some of the most morphologically specialized bony fishes. Much of this specialization relates to their deep-sea milieu:

- Both food and potential mates are scarce in the vast expanse of the deep sea.
- The interior of the sea is dimly lit or completely dark.
- The structureless pelagic environment provides no refuge from predation.

One of the trademark physical features of many stomiiform fishes is their fearsome dentition; their large mouths are filled with enormous fang-like teeth. This allows them to efficiently capture relatively large prey that are infrequently



Larval dragonfish. (Illustration by Joseph E. Trumpey)

encountered. On average, fishes possessing these huge fangs take prey about a third their own size. This would be equivalent to an adult human eating more than 100 hamburgers in a single sitting—and such an equivalent would be an average meal for these fishes! In some cases, the weight of their prey has been known to exceed that of the predator. These fishes have a suite of other adaptations for this type of diet: long, sac-like stomachs; reduced ossification of the anterior vertebrae, allowing the mouth to expand dramatically; and a lack of gill rakers in adults.

Another feature possessed by all but one stomiiform species is the ability to create light (known as bioluminescence) with specialized organs called photophores. Bioluminescence, while rare on land, is quite common in the middle depths of the deep ocean's interior. Bioluminescence results from an oxidative reaction in which an organic molecule, called a luciferin, is raised to a chemically excited state in the presence of the enzyme luciferase. The excited luciferin then decays to the stable state by releasing light (most oxidations release heat). This energy can also be transferred to a fluorescent molecule, which releases light of its own color. Some fishes (e.g., deep-sea anglerfishes) rely on bacterial symbionts for light production. The stomiiforms, however, rely on self-generated, self-regulated luciferin/luciferase reactions occurring within their photophores for light production. The bodies of most stomiiform species bear two serial rows of photophores along each flank. The majority of stomiiform species also bear barbels on their chin. At the end of these barbels are often elaborate, bulb-like bioluminescent organs, thought to serve as "fishing lures." These chin-barbels range in size from less than the head length to as much as 10 times the length of the fish. Many species, particularly those of the genus *Eustomias*, are differentiated solely on the form of the barbel.

In general, stomiiform fishes fall into three major body plans. Plan A, exhibited by the dragonfishes (Stomiidae), is characterized by an elongate body, usually black or dark brown, with dorsal and anal fins placed far back on the body, the previously mentioned chin-barbel, and large teeth that are hinged to accommodate the passage of large prey items. Plan B, exhibited by the bristlemouths (Gonostomatidae), the lightfishes (Phosichthyidae), and maurolicines (Sternoptychidae: Maurolicinae), is characterized by a moderately elongate, minnow-like body, with dorsal and anal fins near mid-body, and large mouths studded with bristle-like teeth. Plan C, exhibited by most marine hatchetfishes (Sternoptychidae: Sternoptychinae), is characterized by a short, deep, highly compressed body with an abdominal keel that gives the body a hatchet-like shape, silvery flanks with a dark back, and a mouth nearly vertical in position. Some species of the latter body plan have tubular eyes directed upwards.

Distribution

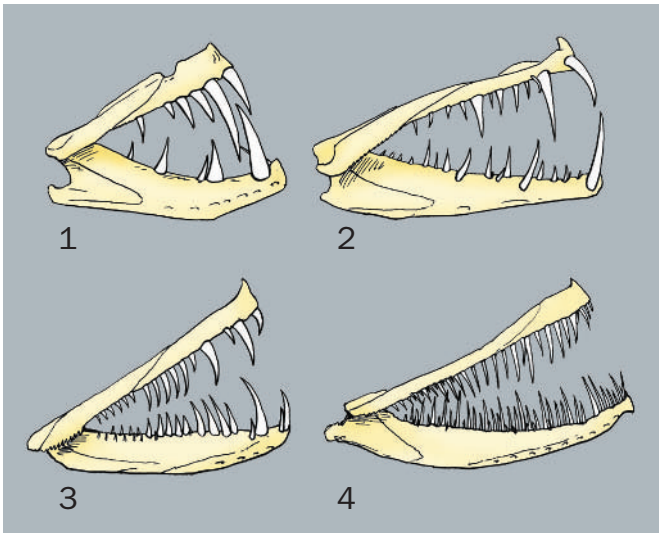
Stomiiform fishes are found over great depths throughout the world's oceans, including the Antarctic seas (but absent in the Arctic Ocean). Highest abundance and diversity is found in tropical seas. Distribution near landmasses is dictated by water depth. Stomiiform fishes are rarely found in waters shallower than 1,650 ft (500 m).

Habitat

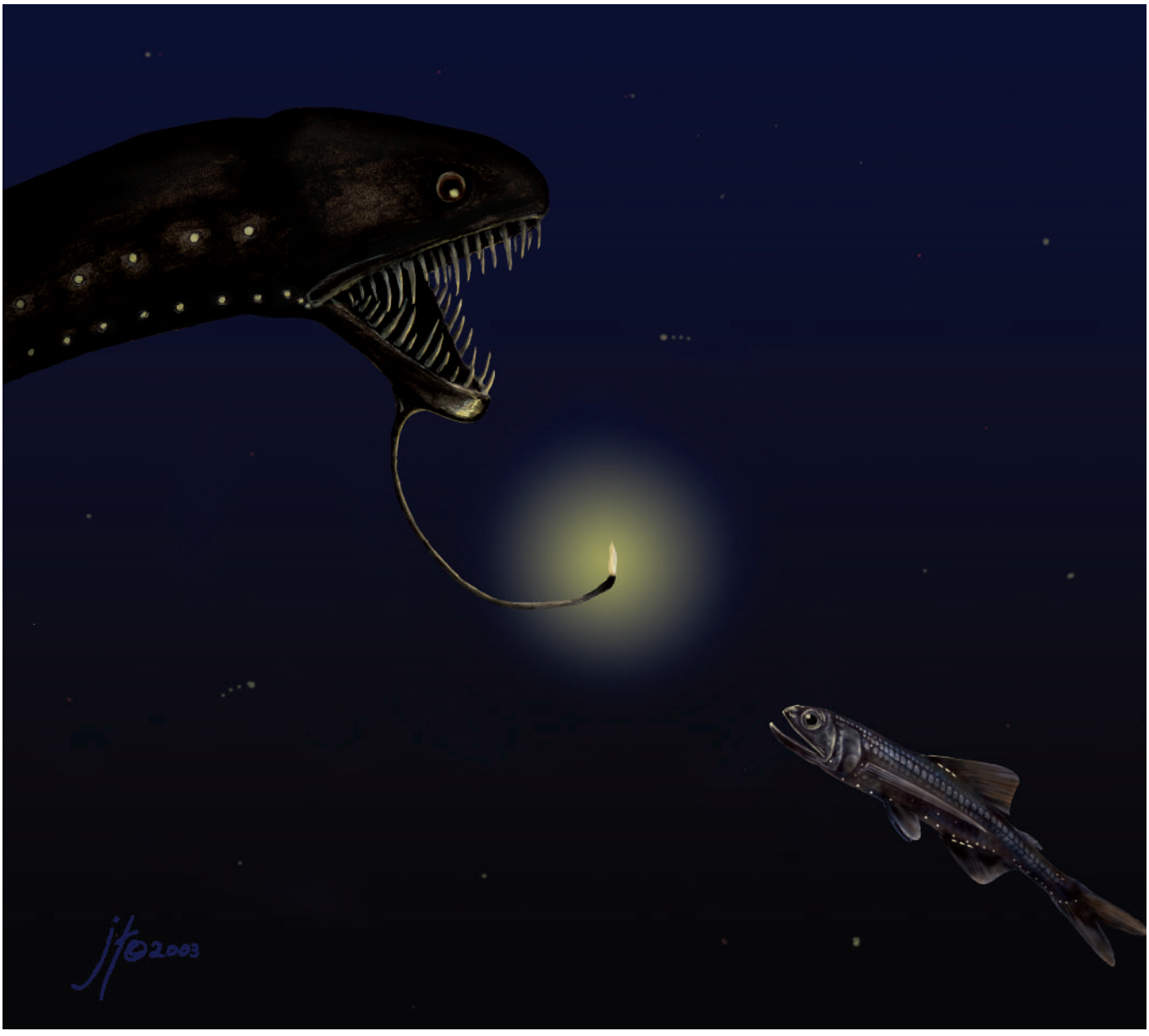
Most species are mesopelagic (residing between 660 and 3,300 ft [200 and 1,000 m] deep), while some others are bathypelagic (residing below 3,300 ft [1,000 m] deep). Stomiiform fishes have been recorded to a depth of more than 14,000 ft (4,270 m). Most species undertake a daily vertical migration, swimming from a daytime depth of 1,600 to 3,300 ft (490 to 1,000 m) to near the surface at night, and then back down again before sunrise. This upward migration is thought to be mainly one for feeding—food in the form of plankton, fish, and other invertebrates is much more plentiful near the surface. Daytime depths, on the other hand, provide refuge from visual predators as well as an energy savings in the colder deep water. This vertical migration, undertaken by most mesopelagic fishes, shrimp, and squid, is the largest animal migration on Earth, and it happens every day in the deep sea.

Behavior

Very little is known of the behavior of stomiiform fishes, mainly because the vast majority of species have never been seen alive. Most specimens have been observed only after being caught in trawls, and the combination of physical trauma,



Jaws and teeth of four dragonfish: 1. *Leptostomias gladiator*; 2. *Grammatostomias dentatus*; 3. *Echiostoma barbatum*; 4. *Tactostoma macropus*. (Illustration by Joseph E. Trumpey)



A female *Melanostomias* dragonfish hunting by luring a lanternfish (*Lepidophanes guentheri*) with her extended luminescent chin barbel. (Illustration by Joseph E. Trumpey)

pressure trauma, and temperature shock is usually lethal. The best-known behavior is that of diel vertical migration, and that is indirectly inferred from differences in abundance as a function of depth and time of day. As of 2001, no stomiiform fishes have been kept alive in aquaria for any length of time.

Feeding ecology and diet

For their size, the stomiiforms are voracious predators. Their feeding ecology falls into two main categories. First is predation on other fishes, shrimps, and squid. Within this category, predation on fishes, particularly lanternfishes (see Myctophidae, this volume), overwhelmingly predominates. Most of the larger stomiiform species feed in this manner (e.g., dragonfishes, loosejaws, viperfishes, and snaggletooths of the family Stomiidae). The second category is planktivory (feeding on microscopic organisms). Within this pattern, predation on copepods (small crustaceans less than 1/8 of an inch [3 mm]) predominates. Most of the smaller stomiiform species feed in this manner (e.g., bristlemouths, lightfishes, and hatchetfishes). As a general rule, planktivorous fishes are always more abundant than higher-level predators. It should be noted that even the higher-level predators are planktivorous during their early life stages.

The manner of feeding of planktivorous stomiiforms is similar to that of all planktivorous fishes—these fishes search small volumes of water, snapping up prey within an appropriate size range as they are encountered. The predacious

dragonfishes, however, use a novel means of capturing prey. Though it has not been directly observed, it is thought that the barbeled forms use their luminescent lures to attract their prey, thus conserving their own energy in a food-limited environment. The posterior fin position of these fishes resembles that of "lie-in-wait" predators, such as pike (Esocidae). That, combined with the muscular control of the barbel, and the otherwise weak body musculature of these fishes, suggests such a strategy. This strategy is most likely the mechanism that has allowed the stomiids to become the top predators of the mesopelagic zone of the world ocean.

Little is known of the predators of stomiiform fishes. Some of the smaller, planktivorous species, such as *Vinciguerria* and *Maurolicus*, are important prey of both pelagic species (e.g., tunas) and outer continental shelf demersal fishes (e.g., Acadian redfish). It is likely that the vast numbers of stomiiform larvae (e.g., *Cyclothone*, *Vinciguerria*) are an important food source in the early life stages of many oceanic fishes. Larger stomiiform species (e.g., dragonfishes) have been found in the diets of benthopelagic fishes (e.g., rattails, roughies) as well as epipelagic fishes (e.g., swordfish) and mammals (e.g., Fraser's dolphin).

Reproductive biology

As with behavior, very little is known of the reproduction of stomiiform fishes. Because of the gear used to capture specimens, few sexually mature individuals of most species have been available for study. It has been theorized that larger, sexually mature individuals are more able to avoid midwater trawls than smaller individuals. That which is known suggests that stomiiforms exhibit a wide range of reproductive modes, mirroring their taxonomic and morphological diversity. It is thought that most stomiiforms spawn at their deeper daytime depths. Higher-latitude species appear to have more discrete spawning seasons than do tropical species, which spawn year-round. Some species spawn several times, while others spawn once and die. Some species have separate sexes, while others mature into males, produce sperm to fertilize eggs, and then later develop into females, producing eggs that are fertilized by younger males. In species with separate sexes, males often have greatly developed olfactory (smell) organs to help in locating females.

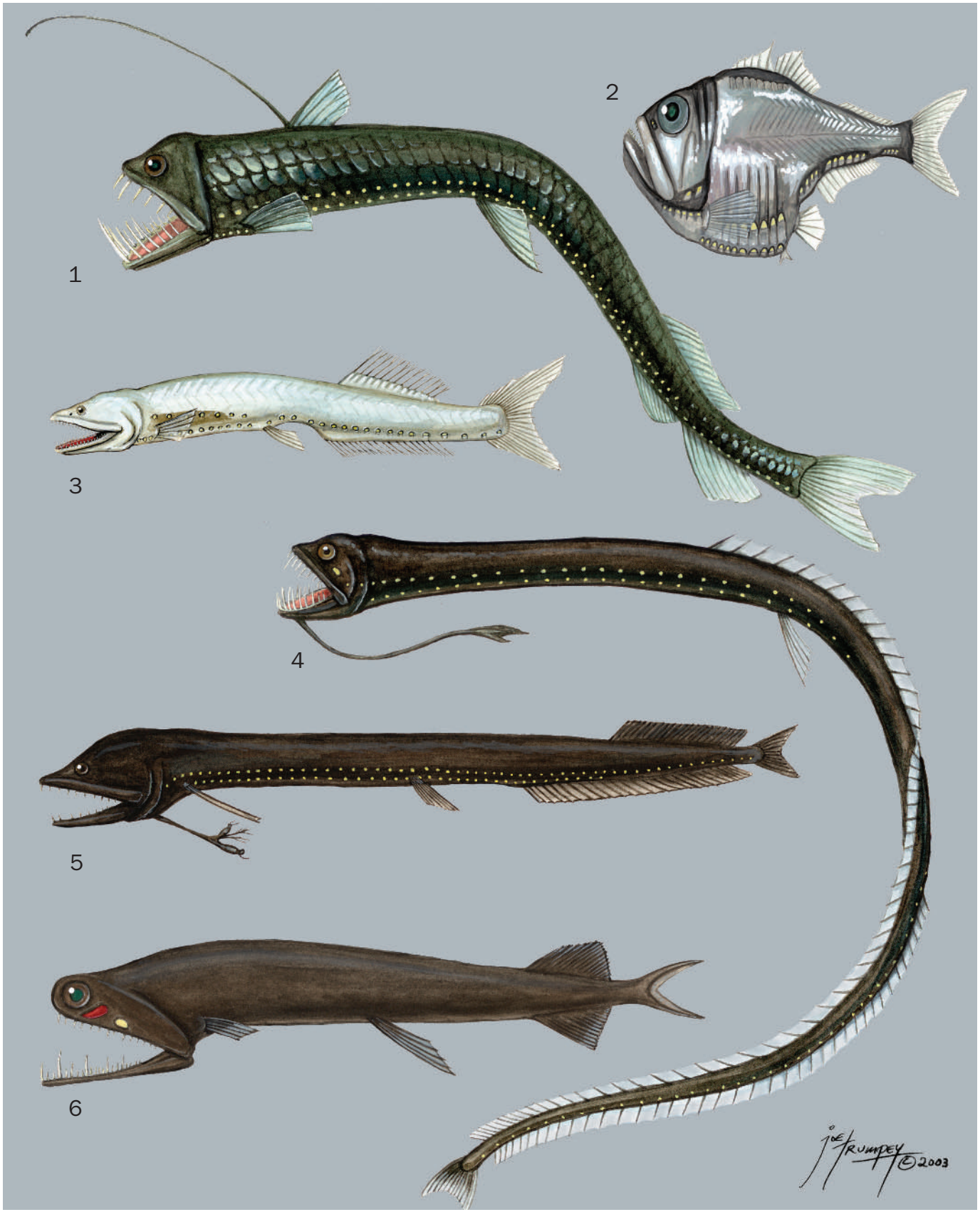
Conservation status

Degradation of the marine environment is a global phenomenon, but as of 2000 no stomiiform fishes are known to be endangered. No species are on the IUCN Red List.

Significance to humans

Due to their bizarre and fearsome appearance, stomiiform fishes have been depicted in myth, literature, and art. Often the forms are exaggerated for effect, but the similarity to extant species suggests that they are often the inspiration.

No direct fishery exists for stomiiform species, though they are an important component of marine food webs. The main value of the stomiiforms is that they are key trophic mediators in the overall economy of the sea. A few isolated ecosystems notwithstanding, life in the ocean begins near the surface, where microscopic plants turn sunlight and carbon dioxide into organic carbon. The consumption of this "primary production" by small planktic animals (zooplankton) serves as the primary means of transforming plant life into animal life. As stated previously, many stomiiform species consume zooplankton directly, while others are the key predators of fishes that consume zooplankton. Thus, through their own consumption, stomiiform fishes are a key link in the transfer of microscopic organic matter to higher trophic levels. For example, the lightfish *Vinciguerria lucetia* is one of the most abundant pelagic fishes in the North Pacific and in turn is an important prey item of commercially fished tunas. To emphasize their importance, it has been claimed that the stomiiform fishes are the most abundant vertebrates on Earth.



1. Viperfish (*Chauliodus sloani*); 2. Silver hatchetfish (*Argyropelecus aculeatus*); 3. Brauer's bristlemouth (*Cyclothone braueri*); 4. Black dragonfish (*Idiacanthus fasciola*); 5. Scaleless dragonfish (*Eustomias schmidti*); 6. Rat-trap fish (*Malacosteus niger*). (Illustration by Joseph E. Trumpey)

Species accounts

Brauer's bristlemouth
Cyclothone braueri

FAMILY
Gonostomatidae

TAXONOMY
Cyclothone braueri Jesperson and Tåning, 1926, Mediterranean Sea.

OTHER COMMON NAMES
English: Bristlemouth

PHYSICAL CHARACTERISTICS
Females to 1.5 in (38.1 mm), males to 1 in (25.4 mm); elongate body, with dorsal and anal fins near midbody; scaleless; nearly transparent, save a few scattered black spots on head; very small eyes; relative to its size it has one of the largest gapes (mouth opening) of any fish; teeth small, bristle-like; males have well-developed olfactory organs to locate females.

DISTRIBUTION
Species occurs throughout Atlantic, but confined to a band at 15–50°S in Pacific and Indian Oceans.

HABITAT
Oceanic and mesopelagic. Depth distribution is age-specific: larvae occur from 30 to 160 ft (9 to 50 m). Adults occur from 825 to 3,000 ft (250 to 900 m) and juveniles in between. This is one of the shallowest living species in an otherwise deep-living genus.

BEHAVIOR
This is one of the few stomiiforms that does not vertically migrate.

FEEDING ECOLOGY AND DIET
Small crustaceans, mainly copepods, are the primary prey.

REPRODUCTIVE BIOLOGY
Thought to spawn once and die; spawning occurs from spring to fall.

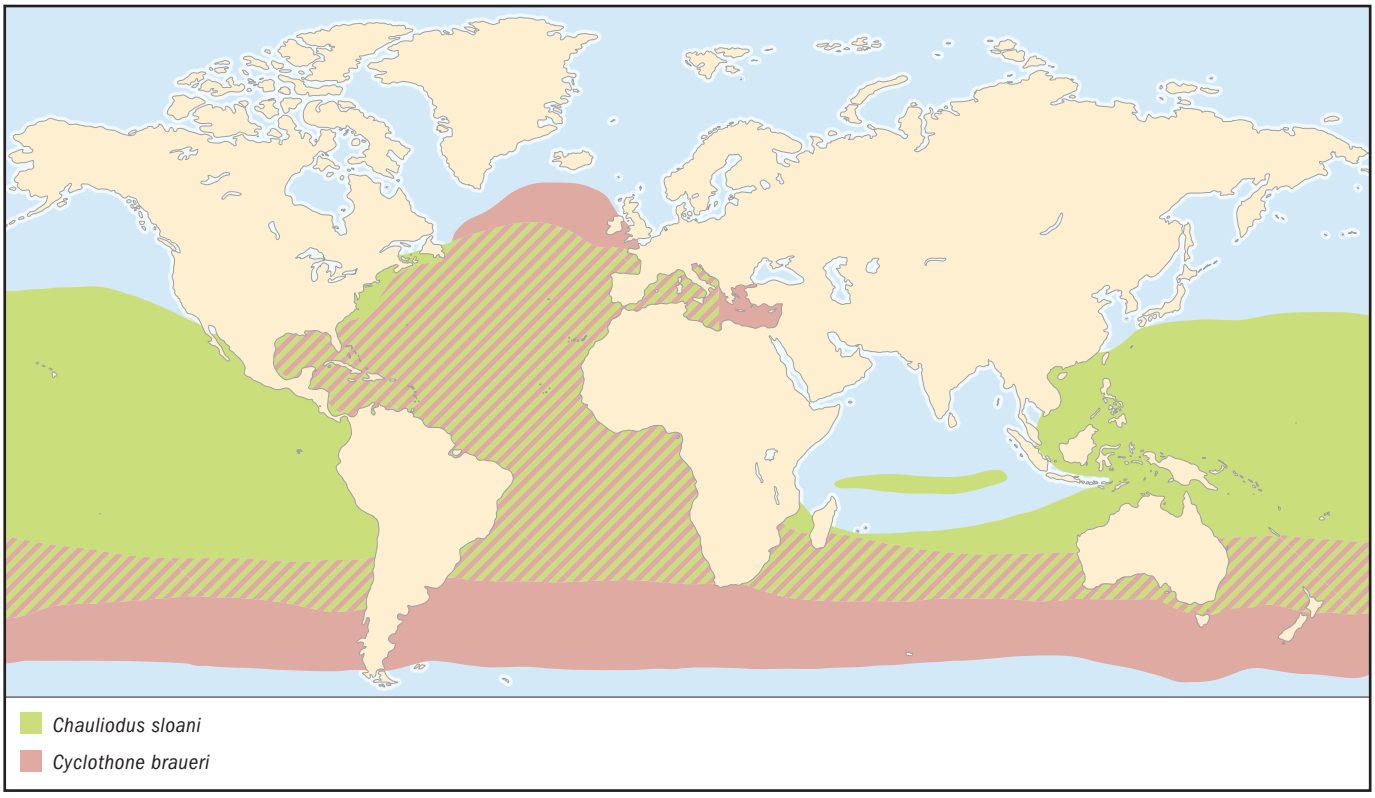
CONSERVATION STATUS
Not threatened.

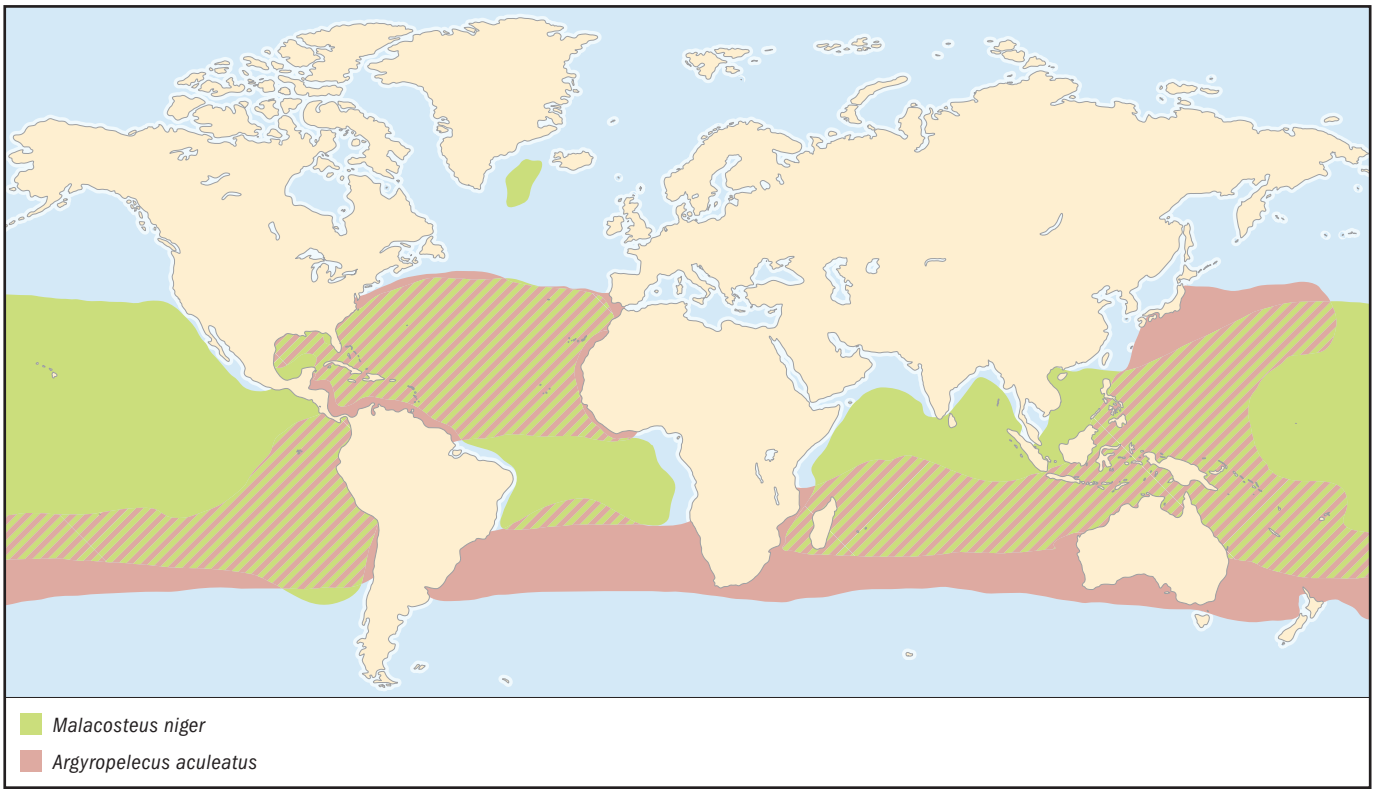
SIGNIFICANCE TO HUMANS
There is no commercial significance. It is claimed to be the most abundant vertebrate on Earth. ◆

Silver hatchetfish
Argyropelecus aculeatus

FAMILY
Sternoptychidae

TAXONOMY
Argyropelecus aculeatus Valenciennes, in Cuvier and Valenciennes, 1830, Azores.





OTHER COMMON NAMES
One of many species called "marine hatchetfish."

PHYSICAL CHARACTERISTICS
Females to 3.3 in (83.8 mm), males to 2.4 in (61 mm); body very deep, laterally compressed, hatchet-like shape derived from abdominal keel-like structure; abdomen bearing well-developed, ventrally directed photophores (these photophores actually account for 21% of the animal's surface area and 15% of its volume); silvery flanks with black back; eyes are tubular and directed upwards; mouth nearly vertical; teeth large, recurved, with two very enlarged canine teeth in lower jaws; scales present, but easily lost.

DISTRIBUTION
This species exhibits an antitropical distribution in the Atlantic, Pacific, and Indian Oceans (i.e., it occurs on each side of the equator, but not directly along the equator). It is much more abundant in the western Pacific than in the east.

HABITAT
Oceanic, mesopelagic; most abundant between 1,000 and 2,000 ft (300 and 600 m) during daylight, 330 and 1,000 ft (100 and 300 m) at night.

BEHAVIOR
This species is a strong vertical migrator. It is known to form discrete, well-defined layers within its vertical range, but it does not form schools.

FEEDING ECOLOGY AND DIET
Feeds mainly at dusk; young fish eat small crustaceans, mainly ostracods, while older fish take larger crustaceans such as euphausiids and decapod shrimp.

REPRODUCTIVE BIOLOGY
Sexes are separate; thought to spawn once and die; spawning takes place year-round, peaking in summer.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No commercial significance; conspicuous component of the "deep scattering layer" registered by the depth sounders of ocean-going ships. ◆

Viperfish
Chauliodus sloani

FAMILY
Stomiidae

TAXONOMY
Chauliodus sloani Bloch and Schneider, 1801, Gibraltar.

OTHER COMMON NAMES
English: Sloane's viperfish.

PHYSICAL CHARACTERISTICS
Length can be up to 13.8 in (350.5 mm). The body is very elongate and compressed with a large head. The body is enclosed in a gelatinous sheath. The dorsal fin is well forward on the body, the second ray of which is elongated and thought to serve as a fishing lure. The anal fin is well back, near the caudal fin. There are adipose dorsal and anal fins. The teeth are rigid and large to enormous (so large, in fact, so as not to fit within

the confines of the mouth, giving this fish a unique perspective—it sees the world through its teeth). There is iridescent yellowish to blue green on the flanks, with a dark back. There are more than 1,500 photophores on the body of this fish. There are five rows of large scales on each side of the body. Juveniles have a short barbel, which degenerates in adults.

DISTRIBUTION
Worldwide in tropical to temperate seas, including the western Mediterranean; absent in the northern Indian Ocean.

HABITAT
Oceanic, meso- to bathypelagic; most abundant between 1,650 and 9,200 ft (500 and 2,800 m) during daylight, with some of the population migrating up to between 70 and 660 ft (20 and 200 m) at night. The rest (non-hungry component) stay at daylight depths.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Juveniles eat small crustaceans, mainly euphausiids, while adults eat fishes, mainly lanternfishes, and occasionally decapod shrimp.

REPRODUCTIVE BIOLOGY
Little is known; spawning takes place year-round with a peak in late winter/early spring.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No commercial significance. Fearsome appearance has inspired depiction in myth, literature, and art. ◆

Scaleless dragonfish
Eustomias schmidti

FAMILY
Stomiidae

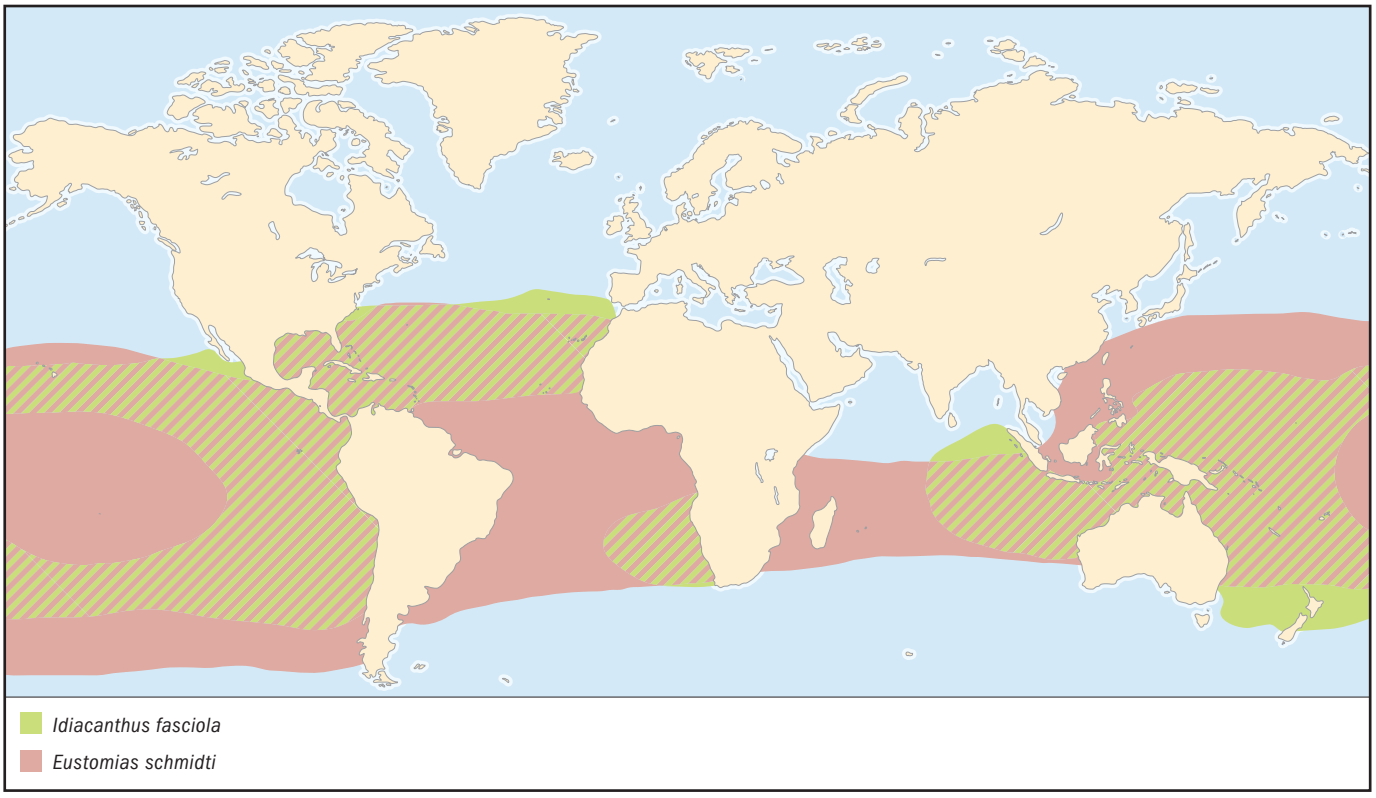
TAXONOMY
Eustomias schmidti Regan and Trewavas, 1930, North Atlantic. One of more than 100 species called "scaleless dragonfish."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
It is recorded to 8 in (203.2 mm). It is very elongate and slender with a long, protrusible snout, as well as a scaleless body uniformly black to dark brown. There are dorsal and anal fins placed far back on the body, with an anal fin that is twice as long as the dorsal. There are fang-like, depressible teeth. The pectoral fins are encased in a black membrane. The belly bears a deep but short groove. The chin-barbel is present and is about half as long as the head, with a main stem and three branches. The main stem bears a bulbous light organ constricted near the tip.

DISTRIBUTION
Worldwide in tropical to subtropical seas; not known from the northern Indian Ocean.

HABITAT
It is oceanic, meso- to bathypelagic. It is most abundant between 2,000 and 3,300 ft (600 and 1,000 m) during daylight, with some of the population migrating up to between 330 and 500 ft (100 and 150 m) at night. The rest (non-hungry component?) stay at daylight depths.



BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Preys on fishes, primarily lanternfishes.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No commercial significance, but of particular interest to deep-sea taxonomists. The true number of valid species in this genus may exceed 100. ◆

Black dragonfish
Idiacanthus fasciola

FAMILY
Stomiidae

TAXONOMY
Idiacanthus fasciola Peters, 1877, Pacific Ocean north of New Guinea. One of several species called "black dragonfish."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
This is among the most extreme cases of sexual dimorphism known. Females are up to 15 in (381 mm); they are extremely elongate and slender, with a long dorsal fin originating before mid-body and an anal fin about half the length of the dorsal. Pectoral fins are present in the larvae and are absent in adults. Pelvic fins are present; there are fanglike, depressible teeth. A chin-barbel is present with an elaborate leaf-like structure at the tip. Males up are to 2 in (50.8 mm). The body resembles postlarval females. Pectoral fins are present in the larvae and absent in adults. The eyes are larger than those of females. Males lack teeth, internal organs, and pelvic fins. Both sexes are uniformly black to dark brown. Females have three longitudinal rows of white tissue on the flanks. There is extraordinary larval development—the eyes of the larvae are borne on long stalks that retreat as the fish grows until the eyes are nested in sockets.

DISTRIBUTION
There is worldwide but disjunct distribution. It is known from the tropical/subtropical Atlantic and Pacific, the eastern South Atlantic, and the eastern Indian Ocean/Indo-Pacific. It is apparently absent or uncommon in the central Pacific.

HABITAT
It is oceanic, meso- to bathypelagic. Females occur between 1,800 and 6,600 ft (550 and 2,000 m) during daylight, while migrating up to as shallow as 165 ft (50 m) at night. Males apparently stay between 3,300 and 6,600 ft (1,000 and 2,000 m).

BEHAVIOR
Females vertically migrate, while males stay deep.

FEEDING ECOLOGY AND DIET
Females prey on fishes, primarily lanternfishes. Males have no teeth or digestive organs—apparently they do not feed after larval transformation, and may live only a few weeks.

REPRODUCTIVE BIOLOGY
Little is known; it may spawn in the summer, probably at great depths. Males have enlarged light organs behind the eyes, apparently to attract females.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Rat-trap fish
Malacosteus niger

FAMILY
Stomiidae

TAXONOMY
Malacosteus niger Ayres, 1848, southeast of Nova Scotia, 42°N–50°W.

OTHER COMMON NAMES
English: Loosejaw.

PHYSICAL CHARACTERISTICS
It is recorded to 9.5 in (241.3 mm). It is somewhat elongate but deeper bodied than dragonfishes, with dorsal and anal fins well back near the caudal fin. The body is uniformly black. It has an enormous mouth, much longer than the skull. There are four pairs of large fangs in the lower jaw. Like other members of this subfamily, this species has no floor in its mouth (i.e., no ethmoid membrane), hence the common name "loosejaw." The body photophores are very small. The eyes are very large, with a large, deep-red photophore under each eye. There is no chin-barbel.

DISTRIBUTION
Worldwide in tropical to temperate seas; has been taken as far north as Iceland in the North Atlantic, but generally occurs south of 40°N.

HABITAT
Oceanic, mesopelagic; occurs between 1,650 and 3,000 ft (500 and 900 m) day and night. This species is the only known non-vertically migrating stomiid.

BEHAVIOR
This is one of the very few animals that can create red light via the large eye photophores, and even more amazing is that it has the ability to see red light (most deep-sea fishes can see only blue/green wavelengths). This confers the ability to search for prey without making itself visible to potential predators. It has been suggested that this fish acquires its red-sensitive visual pigment from the chlorophyll (the green photosynthetic pigment in plants) packaged in the guts of its copepod prey.

FEEDING ECOLOGY AND DIET
Despite its fearsome appearance, this species mainly eats small crustaceans (copepods), while occasionally taking fish and decapod shrimp.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS

There is no commercial significance, but the protein responsible for its red light production has been investigated for possible medical uses. This protein, if it could be synthesized (this species is rare throughout its range) and attached to an antibody, would provide a means of locating and treating cancerous tumors within a human body without the need for invasive surgery. ◆

Resources

Books

Gartner, J., R. Crabtree, and K. Sulak. "Feeding at Depth." In *Deep-Sea Fishes*, edited by David Randall and Anthony Farrell. Boston: Academic Press, 1997.

Hoyt, E. *Creatures of the Deep: In Search of the Sea's "Monsters" and the World They Live In*. Buffalo, NY: Firefly Books, Ltd., 2001.

Periodicals

Fink, W.L. "Phylogenetic Interrelationships of the Stomiid Fishes (Teleostei: Stomiiformes)." *Miscellaneous Publications Museum of Zoology, The University of Michigan* no. 171 (1985): 1–127.

Olney, J.E., G.D. Johnson, and C.C. Baldwin. "Phylogeny of Lampridiform Fishes." *Bulletin of Marine Science* 52 (1993): 137–169.

Sutton, T.T. and T.L. Hopkins. "Trophic Ecology of the Stomiid (Pisces: Stomiidae) Fish Assemblage of the Eastern Gulf of Mexico: Strategies, Selectivity, and Impact of a Top Mesopelagic Predator Group." *Marine Biology* 127 (1996): 179–192.

Tracey T. Sutton, PhD

Aulopiformes
(Lizardfishes and relatives)

Class Actinopterygii
Order Aulopiformes
Number of families 12

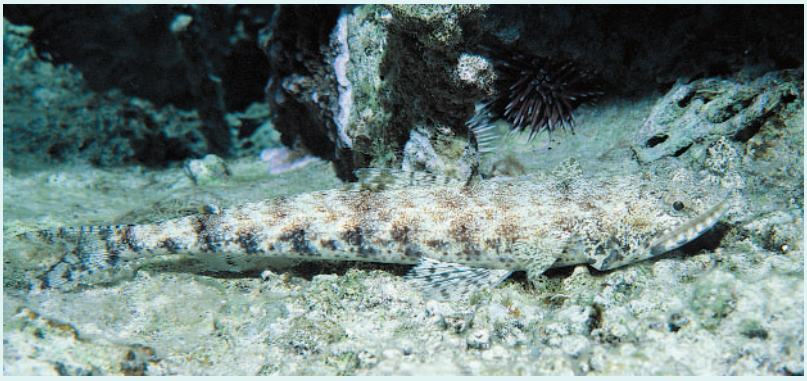


Photo: A slender lizardfish (*Saurida gracilis*) inside the reef in a Tahiti lagoon. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The Aulopiformes have been the subject of numerous systematic revisions over the past 30 years. The most recent one, by Carole C. Baldwin and G. David Johnson, published in 1996, recognized 4 suborders, 12 families, and 43 genera. The suborders include the Synodontoidei (three families, including the lizardfishes and Bombay ducks, the latter group formerly placed in the Harpadontidae and now synonomized), the Chlorophthalmoidei (three families plus two species, *Bathysauropsis gracilis* and *B. malayanus*, with no family assignment), the Alepisauroidei (four families), and the Giganturoidei (two families plus a single species, *Bathysauroides gigas*, with no family assignment). The order is largely monophyletic. (Some familial relationships remain to be resolved.) It traces its ancestry to the Upper Cretaceaous period (135 million years ago). The Aulopiformes share many features with midwater and deep-sea-dwelling Myctophiformes (lanternfishes and relatives), and most species may have evolved over time from life in the pelagic realm to a bottom-dwelling existence.

Physical characteristics

The Aulopiformes are characterized by both primitive and derived or advanced characters. Examples of primitive characters include abdominal pelvic fins with 8–12 rays, the absence of fin spines, the presence of an adipose fin (a structure consisting of fatty tissue located between the dorsal fin and the caudal fin), and scales that are cycloid or rounded in shape. Derived characters include a ductless swim bladder and a maxillary bone that has been excluded from the gape of the jaw. Other characters, present in some groups, include highly modified eyes, hermaphroditism, and well-developed metamorphic stages between larval and juvenile phases. Specialized gill arches further distinguish them from the Myctophiformes. Within the order, body sizes and shapes are diverse and a function of habitat and depth distribution.

Lizardfishes (25 species within the Synodontidae) are cryptically colored, cigar-shaped bottom-dwelling fishes with large, reptilian heads, large mouths, numerous teeth, and an eye placed nearly halfway along the length of the mouth. Bombay ducks (15 species within the Synodontidae) are distinguished by a short and rather rounded snout, long pelvic and pectoral fins, and a medially placed tail lobe formed from lateral line scales. Synodontids are cryptically colored, usually in mottled shades of brown, gray, or red. The Aulopidae (about 10 species) resemble lizardfishes but possess a large dorsal fin; in males, this fin has a first dorsal fin ray that extends well beyond the others. Aulopids also have two small jawbones, the supramaxillae, located along the upper edge of the jawbone. They also are cryptically colored, primarily in shades of green, brown, gray, and red. The monotypic Pseudotrichonitidae are elongate and cylindrical in shape, with a pointed snout, a single elongate dorsal fin, and elongate pelvic fins. Body coloration is exquisite, with a series of red to orangish red patches laterally, and resembling bars when viewed from above. Yellow spots are present just above the lateral line and bordering the red patches, with rows of

Engleman's lizardfish (*Synodus englemani*), eating a fish, near Indonesia, in the Pacific Ocean. (Photo by Animals Animals ©W. Gregory Brown. Reproduced by permission.)

A lizardfish (*Synodus intermedius*) on the sandy bottom, near Bonaire Island in the Netherlands Antilles. (Photo by Mary Beth Angelo/Photo Researchers, Inc. Reproduced by permission.)

faint electric blue spots above and below the lateral line. The fins are pale white to clear with traces of faint iridescent blue.

The Bathysauridae (two species) also resemble lizardfishes but have curved, barbed teeth and a flattened head. Members of the Chlorophthalmidae (12 species), commonly referred to as greeneyes or cucumberfishes (allegedly because they smell like cucumber) have iridescent green or yellow eyes of various sizes. Body color varies from pale green or light brown to a mottled pattern of green, silver, white, brown, and black. The Ipnopidae (about 26 species) have pencil-shaped bodies, flat heads with tiny or poorly developed eyes, and long, thickened fin rays. Body color is variably black, bronze, brown, or dark gray, or mottled in a combination of two or more of these colors. These fishes include the tripod fishes, whose extended pelvic fin rays form two legs of a tripod (with the caudal fin forming the third leg) that allows them to perch above the abyssal bottom. Among the midwater aulopiformes are the large lancetfishes (two species within Alepisauridae), which are distinguished by a long, sail-like dorsal fin that stretches from the head nearly to the adipose fin and may grow to nearly 7 ft (more than 200 cm) in length. These fishes are silvery, pale bronze, or brownish black in color, darker dorsally, and iridescent. Almost as large is the daggertooth (one species within the Anotopteridae), another midwater predator that reaches nearly 5 ft (150 cm) in length but lacks the long sail-like dorsal fin. The daggertooth lacks scales. Body color ranges from silvery to dusty with black on the tips of the pectoral fins, jaws, and also onto the caudal fin.

Also in midwater depths are the telescope fishes (Giganturidae) and pearleyes (Scopelarchidae), which have specialized tubular eyes whose form and function resemble that of a telescope (useful for detecting light in dim surroundings) and allow for forward- or upward-directed vision. Telescope fishes are generally silvery in color, while pearleyes are pale brown. Midwater and deep-water aulopiform fishes that may or may not have tubular eyes and are distinguished by fanglike teeth and a lack of scales include the sabertooth fishes (seven species within Evermannellidae) and the hammerjaw (Omosudidae, one species). The sabertooth fishes range from pale brown to black in color. Hammerjaws are translucent silvery brown, dark brown, or olive-black with hints of silver, white, and pinkish brown. Similar in shape are the waryfishes (Notosudidae), which have both scales and, uniquely, teeth on the upper jawbones or maxillae. Waryfishes are generally pale brown in color, and some species have black fins. The barracudinas (50–60 species within the Paralepididae) are slender and elongate in shape and superficially resemble barracudas; they may grow as large as 39 in (100 cm). These fishes also possess fanglike teeth; a long, pointed snout; and a dorsal fin placed midway along the body. They may or may not have scales. Body color ranges from pale brown to tan or yellowish olive.

Distribution

Members of the Aulopiformes may be found throughout the Atlantic, Pacific, and Indian Oceans, with the exception of most polar waters. They also occur in the Mediterranean, but they appear to be absent from the Black Sea. The Synodontidae typically dwell in warm, shallow waters, although at least one species is found as deep as 1,300 ft (400 m). The Bathysauridae live at depths in excess of 5,250 ft (1,600 m), whereas the Aulopidae is distributed widely, except for the eastern Pacific, in waters near shore to a depth of 3,300 ft (1,000 m). The Pseudotrichonotidae is limited to the shallow waters of Japan and the southeastern Pacific, while the Chlorophthalmidae also may be found in shallow, warm, temperate waters worldwide. Both the Ipnopidae and Giganturidae are distributed widely in deep or abyssal waters. Midwater and bathypelagic species of the families Alepisauridae, Scopelarchidae, Evenmannellidae, Omosudidae, Notosudidae, and Paralepididae all tend to be distributed widely at depths in excess of 1,625 ft (500 m), and some are found down to 3,300 ft (1,000 m). The Anotopteridae range in shallow to deep temperate waters and are rarely found in the tropics.

Habitat

With respect to patterns of habitat use, aulopiform fishes are divided neatly into two camps: bottom-dwelling and water-column or pelagic-dwelling species. Bottom-dwelling families include the Synodontidae (Bombay ducks may be secondarily pelagic), Aulopidae, Pseudotrichonotidae, Chlorophthalmidae, Bathysauridae, and the Ipnopidae. These fishes typically perch or rest upon substrates that include rubble, sand, coral, rock, algae, and even abyssal silt and mud. Some fishes, such as the synodontids, aulopids, and pseudotrichonotids, may bury themselves in sand or rubble. Pelagic families include the Alepisauridae, Anotopteridae, Scopelarchidae, Evenmannellidae, Omosudidae, Notosudidae, and

Paralepididae. These fishes swim actively in the water column even at depths where light is virtually absent.

Behavior

The behavior of most aulopiform fishes is unknown. Many species live at depths that make direct observation of their behavioral patterns extremely difficult if not impossible. Generalizations about some types of behavior can be made, however. For example, bottom-dwelling species are often cryptic and have minimal movement. These characteristics allow them to ambush prey and to avoid predation. Swimming movements of these fishes often are accomplished in short bursts, followed by burying movements in the substrate. Only when they are ambushing prey or escaping predators are their swimming movements rapid. The tripodfishes, which dwell on the abyssal bottom, may "walk" along the bottom with the support of extended pelvic and caudal fins.

Fishes that swim pelagically in the midwater and deep-water realms may do so rapidly in pursuit of prey. Both lancetfishes and daggertooths are powerfully built for swimming and hunting prey. Alternately, some smaller species might hover or rest in the water column and reserve swimming for hunting prey or for vertical migrations at night. The barracudinas swim vertically, with their tails down and their heads up.

Courtship behavior has been observed for some shallow-water species. Observations of lizardfishes have revealed a repertoire of ritualized patterns, some of which also may be used in territorial displays. Among midwater and deep-dwelling species, simultaneous hermaphroditism is common, and self-fertilization is possible, thus precluding the need for courtship behavior.

Feeding ecology and diet

Aulopiform fishes are predators. Bottom-dwelling species, such as the lizardfishes and Bombay ducks, typically feed upon smaller fishes and shrimps that they ambush and capture with their large, tooth-filled mouths. These fishes may bury themselves under the substrate and ambush passing prey just above the bottom and well into the water column. Alternately, they may ambush from perched positions on corals, rocks, or other objects, or they may launch an attack while hovering above the bottom. Regardless, the ambush is executed rapidly and is remarkably successful. Midwater and deep-water pelagic species probably capture prey by hunting or, under dim light conditions, by ambushing passing fishes or larger invertebrates, such as cephalopods or crustaceans. Owing to the colder water temperatures at greater depths, the digestive processes of deep-dwelling species appear to be slow. Thus, these fishes probably feed much less frequently than their shallow-water relatives. Aulopiformes are likely preyed upon by other predatory fishes and also by toothed whales.

Reproductive biology

Members of the Aulopiformes have two mating systems, gonochorism and simultaneous hermaphroditism. Members of the suborder Synodontoidei are gonochoristic, that is, they have separate male and female sexes, and no sex change occurs. Although few detailed studies of reproduction in this suborder exist, its shallow water-dwelling members probably spawn pelagically in the water column and release gametes, which, as fertilized eggs that become larvae, drift in the water column until the larvae settle on suitable habitat and recruit to a local population as a functional member. Courtship and spawning may be seasonal and likely is affected by water temperature. Thus, at higher latitudes courtship is limited to the warmer months of the year. In the tropics, courtship and spawning may proceed all year long.

A lizardfish (*Synodus* sp.) captures a fangblenny (*Plagiotremus* sp.) that was trying to avoid detection by mimicking a cleaner wrasse. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

The lizardfishes mate in pairs before or just after sunset; if the local population size is relatively large and males outnumber females, an alternative tactic may be used. For example, *Synodus dermatogenys* employs lek-like courtship behavior during reproduction. In this system, males form mobile territories in the presence of one or more females. Then they attempt to court a female while defending courtship space around her. Females control spawning. The female may choose to spawn with a single male, or she may allow the participation of additional males who contribute a proportion of their gametes to the fertilization of the gelatinous egg mass that is produced by the female. Furthermore, and unlike most pelagic spawning species that reproduce around sunset, the female may engage in more than one spawning event during a given evening.

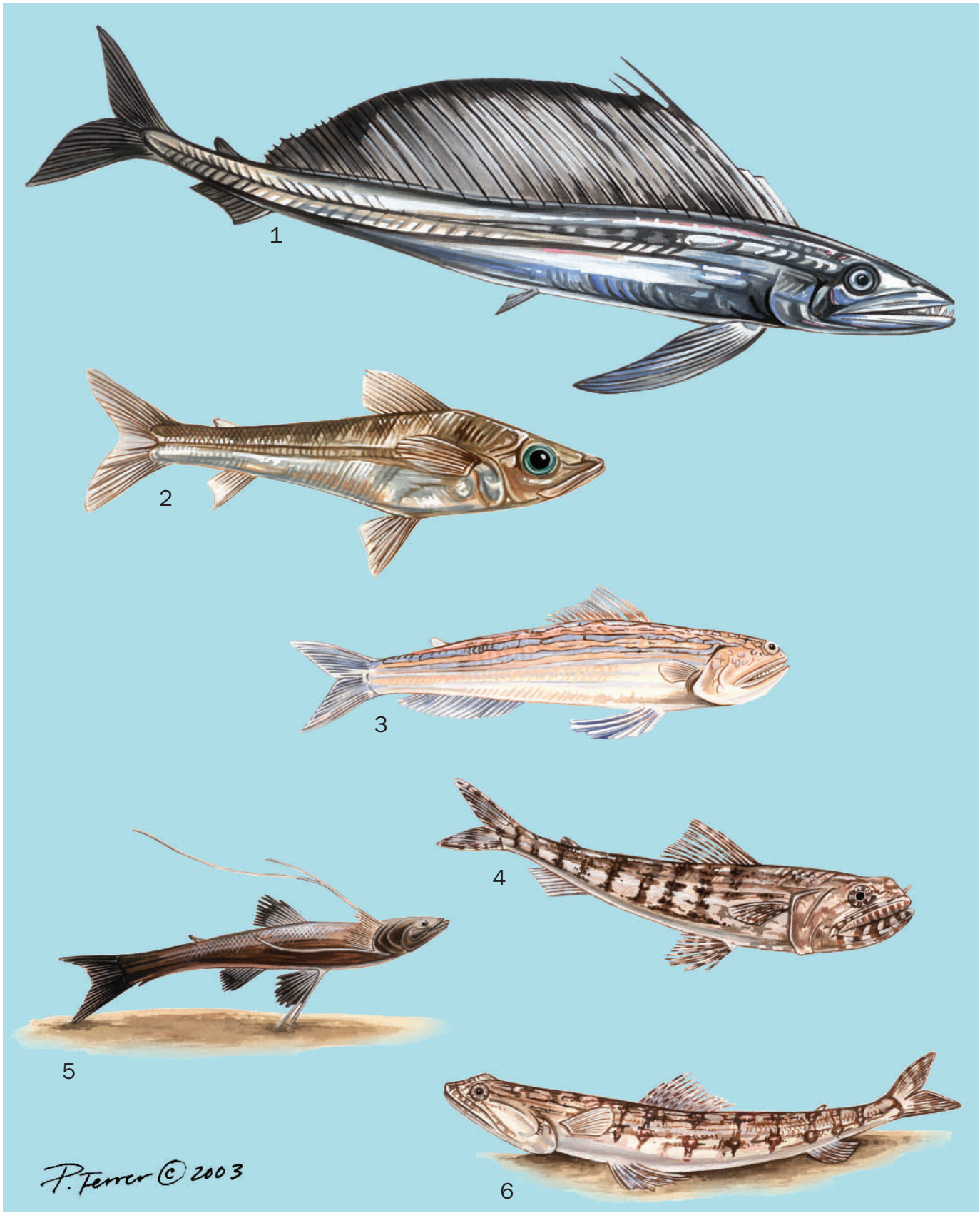
The female also may choose to abort a spawning ascent if she determines that too few males are participating in the ascent. By allowing multi-male spawning, the female may ensure greater fertilization success for her eggs and promote genetic diversity as well. The remaining suborders appear to be capable of being both male and female at the same time, and they can reproduce by self-fertilization. This trait may have allowed for the radiation of species throughout the deep-water realm. Upon maturity, members of the Notosudidae leave the continental slope and spawn pelagically in the open ocean.

Conservation status

No species are listed by the IUCN.

Significance to humans

Although the flesh of shallow-water aulopiform fishes may be generally bony, some species are taken as food in both subsistence and commercial fisheries. Bombay ducks, for example, are caught in the estuaries of India and sold dried in the markets of Mumbai (Bombay), from which their common name is derived. A commercial fishery for other synodontids exists on the trawling grounds of Australia, Hong Kong, and parts of Southeast Asia (where they also are taken with monofilament nets and hook and line). Lizardfishes are sold fresh or salted or in processed form, such as fish balls, fish crackers, or fishmeal. The sergeant baker, *Aulopus purpurissatus* (Aulopidae), is taken by recreational fishers in Australia as well. Similarly, lancetfishes are caught accidentally on lures trolled by anglers in South African waters and elsewhere.



1. Longnose lancetfish (*Alepisaurus ferox*); 2. Greeneye (*Chlorophthalmus acutifrons*); 3. Painted lizardfish (*Trachinocephalus myops*); 4. Slender lizardfish (*Saurida gracilis*); 5. Tripodfish (*Bathypterois quadrifilis*); 6. Clearfin lizardfish (*Synodus dermatogenys*). (Illustration by Patricia Ferrer)

Species accounts

Longnose lancetfish
Alepisaurus ferox

FAMILY
Alepisauridae

TAXONOMY
Alepisaurus ferox Lowe, 1833, off Madeira.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body elongate and compressed, with a very high dorsal fin and a large mouth. The dorsal fin has 30–45 soft rays and the anal fin 13–18 soft rays. The mouth has two erect fangs. The body color is a pale iridescent silver, white, or cream, but darker along the back and upper flanks; at times coloring can contain hints of light blue, green, or red. The fins are brown or black and the lateral adipose keel darkly colored. The adipose fin is positioned posteriorly over the anal insertion. Lacks both a swim bladder and light organs. Reaches over 84.6 in (215 cm) in length.

DISTRIBUTION
In the Atlantic from the Gulf of Maine south to the northern Gulf of Mexico and South America in the west and from Iceland to southern Portugal and the Mediterranean in the east; reappears from Nambia to South Africa. In the Pacific, range extends over the Kuril Islands, Okhotsk Sea, and Japan and in Australia in the west and from Alaska south to Chile in the east. Apparently not recorded from the Indian Ocean.

HABITAT
Mesopelagic and epipelagic waters from more than 5,900 ft (1,800 m) to the surface, depending upon the time of day. This species occasionally ventures inshore.

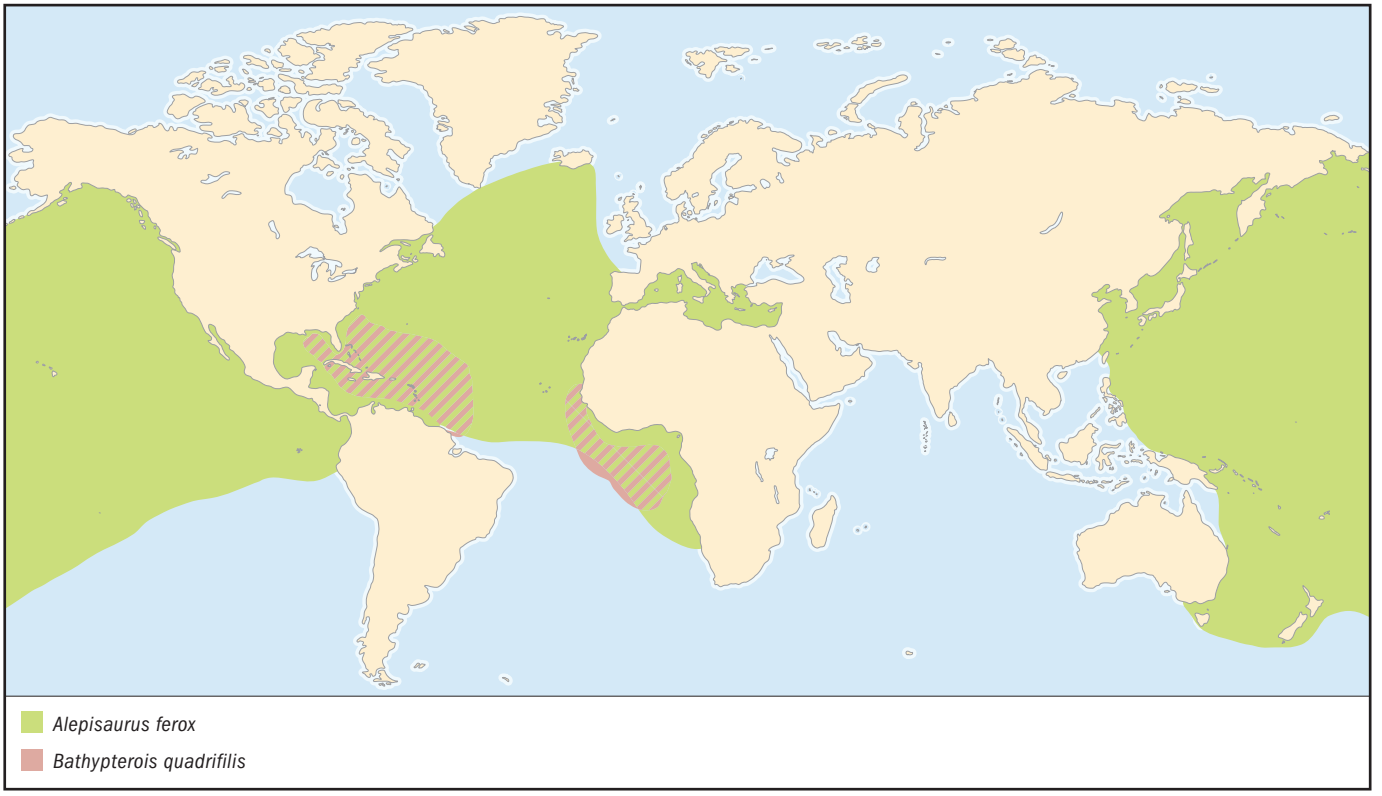
BEHAVIOR
Not much is known about the behavior of this species. A nocturnal species that migrates vertically toward the surface at night and descends into deep water during the day.

FEEDING ECOLOGY AND DIET
Preys upon cephalopods, crustaceans, and fishes; will also take tunicates from the bottom. Preyed upon by sharks, albacore, and yellowfin tuna, opahs, and, close to shore, fur seals.

REPRODUCTIVE BIOLOGY
Not well known. Likely produces pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken incidentally but not esteemed as food. ◆



Greeneye
Chlorophthalmus acutifrons

FAMILY
Chlorophthalmidae

TAXONOMY
Chlorophthalmus acutifrons Hiyama, 1940, Kumano-nada, Japan from 1,640 ft (500 m).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body elongate; the contour of the head concave dorsally and elevated to the dorsal fin. The dorsal fin has 10–12 soft rays and the anal fin 9–11 soft rays. Eyes are greenish. There is a light organ surrounding the anus. The body color is a pale, iridescent green, with a somewhat pale belly. The caudal fin is forked and, like the other fins, pale in color. Reaches 11.8 in (30 cm) in length.

DISTRIBUTION
Western Pacific, from southern Japan to the Philippines.

HABITAT
Dwells on the bottom of moderately deep waters.

BEHAVIOR
Not well known. Probably somewhat similar to that of shallow water dwelling lizardfishes.

FEEDING ECOLOGY AND DIET
Carnivorous, feeding upon fishes.

REPRODUCTIVE BIOLOGY
Not well known. Likely produces pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Of minor commercial importance as a food fish. ◆

Tripodfish
Bathypterois quadrifilis

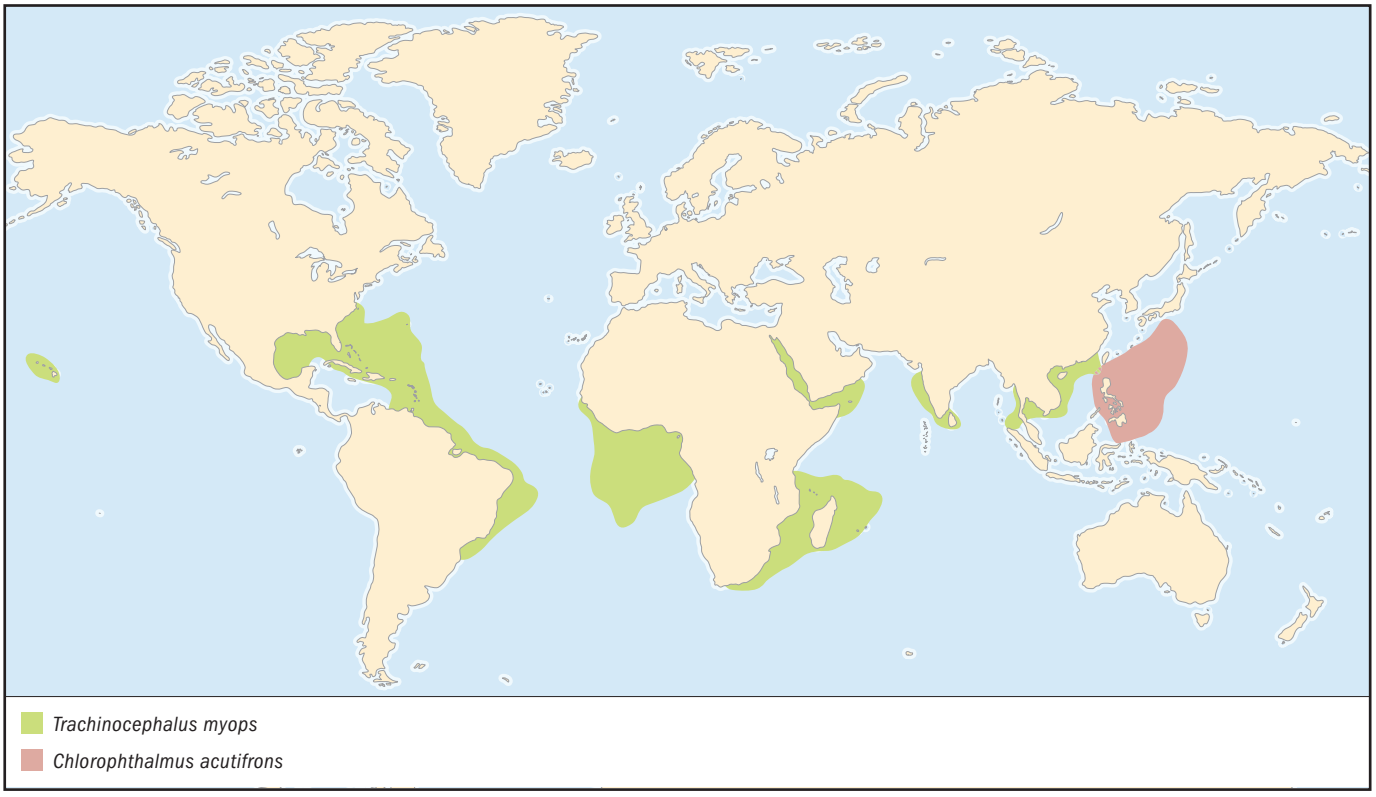
FAMILY
Ipnopidae

TAXONOMY
Bathypterois quadrifilis Günther, 1878, off Brazil.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body elongate and compressed, with the tip of the upper jaw extending posteriorly beyond the orbit of the eye. Pectoral, pelvic, and caudal fin rays are all quite elongate (although the latter less so) and firm; when erect, they function like a tripod, thus allowing this species to balance itself above the bottom. Color somewhat bronze to pale, with grayish hues on the head and ventral surface and along the lower back. Fins somewhat pale. The dorsal fin has 14–15 soft rays and the anal fin 9–10 soft rays. Two of the pelvic rays reach the origin of the anal fin. The species reaches 7 in (18 cm) in length.

DISTRIBUTION
Deep water of the Atlantic Ocean, in the Gulf of Guinea off Africa and also from the western Atlantic in the region



between 35° north and 10° south latitude (includes both the Gulf of Mexico and the Caribbean).

HABITAT
This is a bathydemersal species that dwells between 1,310 and 4,650 ft (400–1,410 m) on sand, rubble, silt, and other bottom sediments.

BEHAVIOR
This species is capable of "walking" on the bottom by using its modified fins, which act like a tripod.

FEEDING ECOLOGY AND DIET
Carnivorous, feeding upon smaller fishes and crustaceans that it ambushes on the bottom.

REPRODUCTIVE BIOLOGY
A synchronous hermaphrodite. Eggs are likely pelagic, as are the larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
No commercial importance but an obvious curiosity to science. ◆

Slender lizardfish
Saurida gracilis

FAMILY
Synodontidae

TAXONOMY
Saurida gracilis Quoy and Gaimard, 1824, Hawaiian Islands and Mauritius.

OTHER COMMON NAMES
English: Graceful lizardfish, slender grinner; German: Graziler Eidechsenfisch; Japanese: Madara-eso.

PHYSICAL CHARACTERISTICS
Grows to 12.4 in (31.5 cm). Has 11–12 dorsal rays, 9–10 anal rays, and 12–14 pectoral fin rays (usually 13). There are 50–52 lateral line pores. Head distinguished by several rows of villiform teeth.

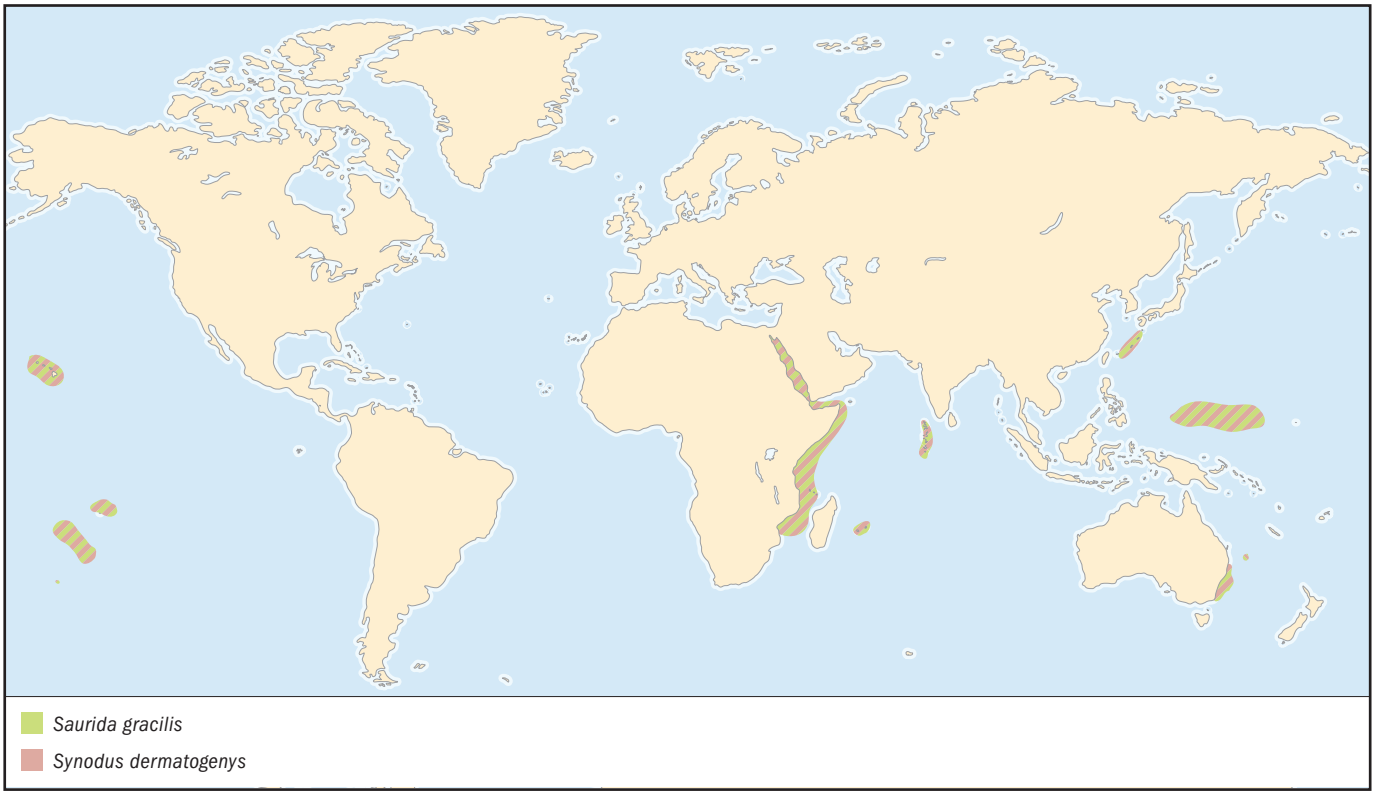
DISTRIBUTION
Tropical waters from the Red Sea east to the Hawaiian Islands, the Marquesas, Rapa Island, and Ducie Island; also from the Ryukyu Islands (Japan) south to southeastern Australia and Lord Howe Island.

HABITAT
This lizardfish is found in depths of 3–405 ft (about 1–135 m) but most commonly in shallow sand and rubble flats of lagoon and protected seaward reefs.

BEHAVIOR
Usually solitary but may be seen in pairs. Perches on ledges and rocks or buries itself in the sand or rubble. Reportedly active at night.

FEEDING ECOLOGY AND DIET
An ambush predator that feeds upon smaller fishes near the bottom or at depths to 15 ft (5 m) into the water column.

REPRODUCTIVE BIOLOGY
The reproductive behavior and ecology of this species are largely unknown; it likely engages in paired courtship and pelagic spawning just before or after sunset. Eggs and larvae are pelagic.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken only incidentally in subsistence, artesanal, or commercial fisheries. Not generally valued as a food fish but may be processed into fish meal, fish cakes, or other processed forms. ◆

Clearfin lizardfish
Synodus dermatogenys

FAMILY
Synodontidae

TAXONOMY
Synodus dermatogenys Fowler, 1912, Hawaiian Islands.

OTHER COMMON NAMES
English: Sand lizardfish, two-spot lizardfish; German: Sand-Eidechsenfisch.

PHYSICAL CHARACTERISTICS
Grows to 7.1 in (18 cm). Has 10–13 dorsal rays, 8–10 anal rays, and 11–13 pectoral fin rays. There are 56–61 lateral line pores and 5.5 scale rows above the lateral line. Yellowish streaks between each pelvic fin ray and at least eight diamond-shaped marks along each flank.

DISTRIBUTION
Tropical waters from the Red Sea east to the Hawaiian Islands and southeast to the Marquesas, the Tuamotu Archipelago, and Rapa Island. Also from the Ryukyu Islands (Japan) south to southeastern Australia and Lord Howe Island.

HABITAT
This lizardfish is found in depths of 3–210 ft (about 1–70 m) on sand and rubble of lagoon and seaward reefs.

BEHAVIOR
Usually solitary but may be seen in mating groups. Buries in sand to ambush prey and escape predators.

FEEDING ECOLOGY AND DIET
An ambush predator that feeds upon smaller fishes.

REPRODUCTIVE BIOLOGY
If population densities are relatively high and males outnumber females, this species engages in lek-like courtship and group or paired spawning; otherwise, it engages in paired courtship and spawning. Males in leks defend mobile territories against rival males while courting females. Females may spawn more than once per day and appear to regulate the number of males participating in a spawning event and, hence, the relative proportion of eggs fertilized by each participating male. Spawning is pelagic, just before or after sunset, and the spawning ascent results in the release of a gelatinous cloud of eggs. The eggs, as in all lizardfishes, typically are large and spherical, are marked by a pattern of hexagonal meshing on the surface, and have only a few oil droplets or none at all. The eggs hatch after two to three days. Spawning may be daily (low tropics) or seasonal (higher latitudes), depending on water temperature. Larvae are long, slender, and pelagic and undergo a well-developed metamorphosis into juveniles.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken only incidentally in subsistence or artesanal fisheries. Not generally valued as a food fish, except in Southeast Asia. ◆

Painted lizardfish
Trachinocephalus myops

FAMILY
Synodontidae

TAXONOMY
Trachinocephalus myops Forster, 1801, Saint Helena.

OTHER COMMON NAMES
German: Gemalter Eidechsenfisch; Japanese: Oki-eso.

PHYSICAL CHARACTERISTICS
Grows to nearly 14 in (38 cm). Has 11–14 dorsal rays; 13–18 anal rays, and 11–13 pectoral fin rays. There are 51–61 lateral line scales and 3.5 scales above the lateral line. Pectoral fin reaches line from origin of dorsal fin to the origin of the pelvic fin. Has a single series of slender needlelike teeth along entire jaws.

DISTRIBUTION
Tropical waters of the Atlantic, Pacific, and Indian Oceans.

HABITAT
Usually on sand in estuaries and subtidal shores to a depth of more than 600 ft (200 m).

BEHAVIOR
Solitary, paired, or in loose aggregations (the latter possible mating groups). Buries itself in the sand with only the eyes emerging.

FEEDING ECOLOGY AND DIET
Ambushes smaller fishes near the bottom or in the water column.

REPRODUCTIVE BIOLOGY
The reproductive behavior and ecology of this species are largely unknown. Pairs have been observed courting in the water column, a departure from the benthic courtship seen among members of the pelagic-spawning genus *Synodus.* Eggs and larvae are probably pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken incidentally in subsistence, artesanal, or commercial fisheries. Not generally valued as a food fish, except in Southeast Asia. ◆

Resources

Books

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96921 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Terry J. Donaldson, PhD

Myctophiformes
(Lanternfishes)

Class Actinopterygii
Order Myctophiformes
Number of families 2

Photo: A brooch lanternfish (*Benthosema fibulatum*) seen in the daytime in Bali. (Photo by Animals Animals ©R. Kuiter, OSF. Reproduced by permission.)

Evolution and systematics

The earliest fossil records for the family Myctophidae are reported from the Miocene epoch of the Upper Tertiary period approximately 23 million years ago.

The current order has undergone a series of taxonomic revisions over the years. Until about 1940, the neoscopelids were included as a subfamily within the Myctophidae. Both were included as members of the order Myctophiformes (two suborders containing some 15 families), first erected in 1911. The Myctophiformes were relegated to a suborder within the Salmoniformes in the sweeping systematic revision of living teleost fishes in the mid-1960s (the original *Grzimek's* account of myctophids places them in that order), but this received little support. By the early 1970s, the Myctophiformes were reestablished as a separate order, with the neoscopelid and myctophid families being recognized as a distinct suborder, the Myctophoidei. An extensive re-view of the myctophoid families in the mid-1990s resulted in the establishment of a separate superorder, the Scopelomorpha, containing the order Myctophiformes. As constructed, the Myctophiformes were reduced to the families Neoscopelidae and the Myctophidae, with the other genera of the former Myctophiformes placed in a sister group, the Acanthomorpha.

As the order is currently organized, the Neoscopelidae ("blackchins") represent the more generalized morphology, and only three genera and six species are currently recognized. The Myctophidae ("lanternfishes") are believed to be derived from the neoscopelids, and are a far more diverse family of some 230 to 250 species in 32 currently recognized genera. In the most recent review of the family, two subfamilies are recognized, the Myctophinae (13 genera) and the Lampanyctinae (19 genera).

Physical characteristics

Neoscopelids and myctophids are generally small fishes, with the largest species in both families not exceeding 11.8 in (300 mm) standard length (SL, measured from tip of the snout to base of tail). Most myctophid species are much smaller, usually less than 3.1 in (80 mm) SL at maximum size. The most common members of both families resemble anchovies, with very large terminal to subterminal mouths and large eyes. In fact, in some Russian papers, myctophids are referred to as "luminescent anchovies." The jaws bear numerous tiny teeth, and in most species, the gills bear enlarged bladelike gill rakers along the first gill arch, the number of which is used as a taxonomic character for differentiating species.

Probably the most distinctive characteristic of most species of both families are the numerous light-producing organs (known as photophores) covering the body. The photophores are concentrated along the lower sides and ventral (belly) region, as well as on the head. The photophores are arranged in patterns that are distinctive to each species. In addition to photophores, many species of myctophids bear luminescent scales and glands in particular regions. The production of light in the glands and photophores is the result of a chemical oxidation reaction that can be triggered and regulated by the animal's nervous system. The light produced is in the blue-green range and in some of the glands can produce a burst of light like a camera flashbulb going off, enough to illuminate the interior of a darkened submersible!

Both families exhibit two general body morphologies among different genera and species. One is a robust, firmly muscled body, the other, a watery, flabby body with weakly developed skeletons and muscles. These body forms are believed to relate to vertical distribution and habits.

The rays of all fins are soft. An adipose fin is present in all species. Pelvic fins are forward of the mid-body, usually under the beginning of the single dorsal fin. Pectoral fins are quite variable in length among different genera, but in all cases are attached along the lower one-third of the body. In neoscopelids and some species of myctophids, the pectorals are long and sweeping, in some species extending almost the length of the body, while a number of soft-bodied species in the genus *Lampanyctus* have such small, delicate pectorals that they are almost unnoticeable.

The bodies are fully covered with deciduous scales, which are cycloid (smooth) in most species, although members of a few genera (most notably, *Myctophum*) bear ctenoid (ctenii are small toothlike structures) scales. These scales blow off the body in a glittering cloud when the fish is struck by objects such as a net, submersible, or predator. Specialized scales cover the photophores. Some scales in myctophid species are covered with a luminescent gland.

Coloration observed in living specimens ranges from a brilliant metallic bronze in the neoscopelid genus *Neoscopelus* to a countershaded dark blue-black on the dorsal surface and mirror-like silvery sides and ventral surfaces in most myctophid species. However, some deep-dwelling myctophid species, including members of the genus *Lampanyctus* and *Taaningichthys*, are dark brown or black. Photophores on freshly captured specimens appear silver, reddish, or in species of the genus *Diaphus*, deep sapphire blue.

Distribution

The neoscopelid species are mainly found in deep waters in tropical and subtropical regions. Two of the three genera have representatives found in all three oceans, but the monotypic genus *Solivomer* is thus far only known from deep waters off the Philippines.

In contrast, myctophids are found in all oceanic waters of the world, with endemic species occurring in all but the Arctic Ocean. In his comprehensive treatise *Developments in Deep-Sea Biology*, Marshall (1980) stated, "...lantern-fishes are so successful that a sizeable net towed at mesopelagic levels almost everywhere in the ocean is almost bound to catch them. If, as seems very likely, they have not colonized the Arctic Sea, then it is improbable that other groups of midwater fishes have gained a footing."

Species diversity of myctophids is highest at tropical-subtropical latitudes, while abundances of individual species appear greatest at temperate and higher latitudes.

Habitat

Both neoscopelids and myctophids are considered oceanic, that is, they normally inhabit waters oceanward of the continental shelf edge. As adults, species of both families are primarily mesopelagic inhabitants, usually found between 660 and 3,330 ft (200 and 1,000 m). Distribution of some species (*Scopelengys tristis* in the Neoscopelidae, and all *Taaningichthys* species in the Myctophidae) may extend into the upper bathypelagic, perhaps to about 3,960 ft (1,200 m) or so. Several neoscopelid and a number of myctophid species are thought to be (or to become at some point in their lives) benthopelagic, spending part of their life cycle near, but not in contact with, the bottom.

Larval myctophids are primarily epipelagic. The few studies that have been done on their distribution shows them to mainly occur between about 165 to 825 ft (50 to 250 m) depth.

Behavior

One of the most notable behaviors observed among many mesopelagic animals, especially myctophid fishes, is that of diel vertical migration. With the exception of the deep mesopelagic genus *Taaningichthys*, adolescents and adults of all myctophid species move from mesopelagic depths into very shallow epipelagic waters at night. In fact, a number of species can be dip-netted from the very surface waters. They do this to feed and to lay their eggs in the food-rich shallower surface waters, usually above 330 ft (100 m) depth. Ascent and descent have been estimated to take about 2 hours each for a species population to shift from daytime to nighttime depths and *vice versa*.

Let us put this remarkable achievement into a human perspective. A 2-in (50-mm) myctophid migrating from 2,300 ft (700 m) to 330 ft (100 m) and back travels about 12,000 body lengths in four hours. This would be equivalent to a 6-ft (180-cm) human having to travel 72,000 ft or 13.6 mi (2.2 km) on foot in 4 hours *every night*.

Within any migratory population, it is believed that most individuals undertake this movement over each diel cycle. However, in most species, larvae are nonmigratory. Newly metamorphosed juveniles also have been shown to either remain shallow and nonmigratory, or to descend into deep water, after which they remain nonmigratory for a period of time. Other restrictions on migration also have been demonstrated. Researchers have shown that in some species, old individuals may restrict or cease migrating, and gravid females often reduce the extent of migration. In addition, it has been shown that physical conditions such as solar eclipses, the degree of moon fullness, clarity of the night sky and the presence of strong current boundaries all affect the extent of vertical migration.

Observed swimming behavior among myctophids takes two forms, depending on the body type. Robust-bodied species swim in short bursts, propelled by a rapid closing of the tail fin rays and flick of the tail. In general, these are the strongest migrators, with the widest difference in day and night vertical distribution. The flabby-bodied forms tend to move with a slow eel-like wriggling of the entire body. These species tend to be found in the deeper mesopelagic depths and migrate shorter distances.

Neoscopelids are not common animals, and little is known about their behavior or habits. An individual of the neoscopelid *Neoscopelus microchir* was observed from a submersible in a head down position with its large pectorals held straight out from the sides. It evaded the submersible by swimming downward in short bursts similar to the robust myctophid behavior and remaining in a head down posture.

Feeding ecology and diet

As with other aspects of their biology, specific feeding habits of neoscopelids are unknown.

Historically, myctophids have been characterized as opportunistic feeders with a generalized diet of small crustacean zooplankton. While it is true that almost all myctophid species can be characterized as crustacean zooplanktivores, a few detailed studies have shown that myctophids actually exhibit a high degree of size and species selectivity. Prey are consumed whole.

Post-metamorphic and adult myctophids are mainly nocturnal feeders. Indeed, a longstanding hypothesis regarding their diel migration is to enter the food-rich surface waters at night to feed. In contrast, a recent study conducted on 14 species of myctophid larvae showed that all but one species fed during the day, with one species showing no temporal response to feeding. Most larvae fed on very small crustacean zooplankton, but several species also included gelatinous zooplankton such as salps as an important or primary prey resource.

While the presence of neoscopelids as prey items of other species has rarely been reported, myctophids are important diet components for a number of different predators. Myctophids form consistent to significant prey items for a number of mesopelagic predatory fishes including many of the stomiiforms (dragonfishes, snaggletooths, and viperfishes). Squids have been observed feeding on myctophids on numerous occasions, and myctophid otoliths have been recovered from squid stomachs as well. A number of marine mammal species have been found with significant numbers of myctophid remains in their stomachs. Reported stomach contents of the beaked whale genus *Mesoplodon* from the western North Atlantic include large numbers of the myctophid *Ceratoscopelus maderensis* as well as squid remains.

Myctophids have also been reported as regular diet components for a number of oceanic seabirds, especially species that feed at night and presumably capture the myctophids as they themselves feed in shallow waters at night. One group of predatory animals in which lanternfishes are rarely reported are epipelagic fishes such as tunas (family Scombridae) and their relatives. This is because scombrids are daytime visual predators, and except for some deep diving species, such as large bluefin tuna, they are not feeding when myctophids are present in their habitat. A second hypothesis regarding the diel vertical migrations of myctophids and other mesopelagic migrators is that the migration is driven by a downward descent in daytime to avoid epipelagic predation, with a return to food-rich epipelagic waters at night for feeding and reproduction.

Reproductive biology

Neoscopelids are apparently dioecious, but beyond this, no information is available on their reproductive habits.

The myctophids are also dioecious, and a number of genera also exhibit sexual dimorphism. The type of dimorphism varies among these genera and even among populations.

In a number of genera (e.g. *Benthosema*, *Hygophum*, *Myctophum*), males possess a supracaudal luminescent gland (just in front of tail on the upper surface of body), while females possess an infracaudal gland (in front of tail on lower surface). In the diverse genus *Diaphus*, most species have enlarged luminescent glands on their heads (called supraorbital glands or "headlights"), which are typically much larger in males. Males and females of the monotypic genus *Notolychnus valdiviae* can be distinguished by the noticeably larger eyes of the males. Another pattern of dimorphism is found in some species such as *Ceratoscopelus warmingii* and *Electrona antarctica*, in which males are distinctly smaller than females at maximum size.

Although there are exceptions to the rule, lower latitude species tend to spawn year-round, whereas higher latitude species typically spawn during a restricted period once per year. Lower latitude species tend to live 1 year or less, whereas higher latitude species may live 3–4 years.

Conservation status

There are no known conservation measures specific to these families. No species from either family is listed by the IUCN.

Significance to humans

From a commercial standpoint, the significance of these families is minimal and mostly indirect. Several fisheries have been or are being conducted for myctophids, in particular by the former Soviet Union, Republic of South Africa, and most recently, in the Arabian Sea by Iran. Myctophid catches are mainly processed to form fish meal, which is used as poultry feed and also as a crop fertilizer. In a fashion similar to sardines and anchovies, one may purchase tins of myctophids packed in oil.

In an ecosystem sense, however, the impact of myctophids may be especially enormous. Studies show that myctophids occupy a central role in open ocean energy transfer, especially between surface and deep ocean waters. They are important prey (in some cases, the most important) for a number of marine mammals. Damage to, or loss of, myctophid populations could have serious repercussions for many other organisms in open ocean food webs.

Species accounts

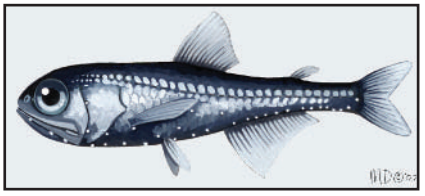
Skinnycheek lanternfish
Benthosema pterotum

FAMILY
Myctophidae

TAXONOMY
Scopelus pterotus Alcock, 1890, Bay of Bengal.

OTHER COMMON NAMES
Japanese: Iwa-hadaka.

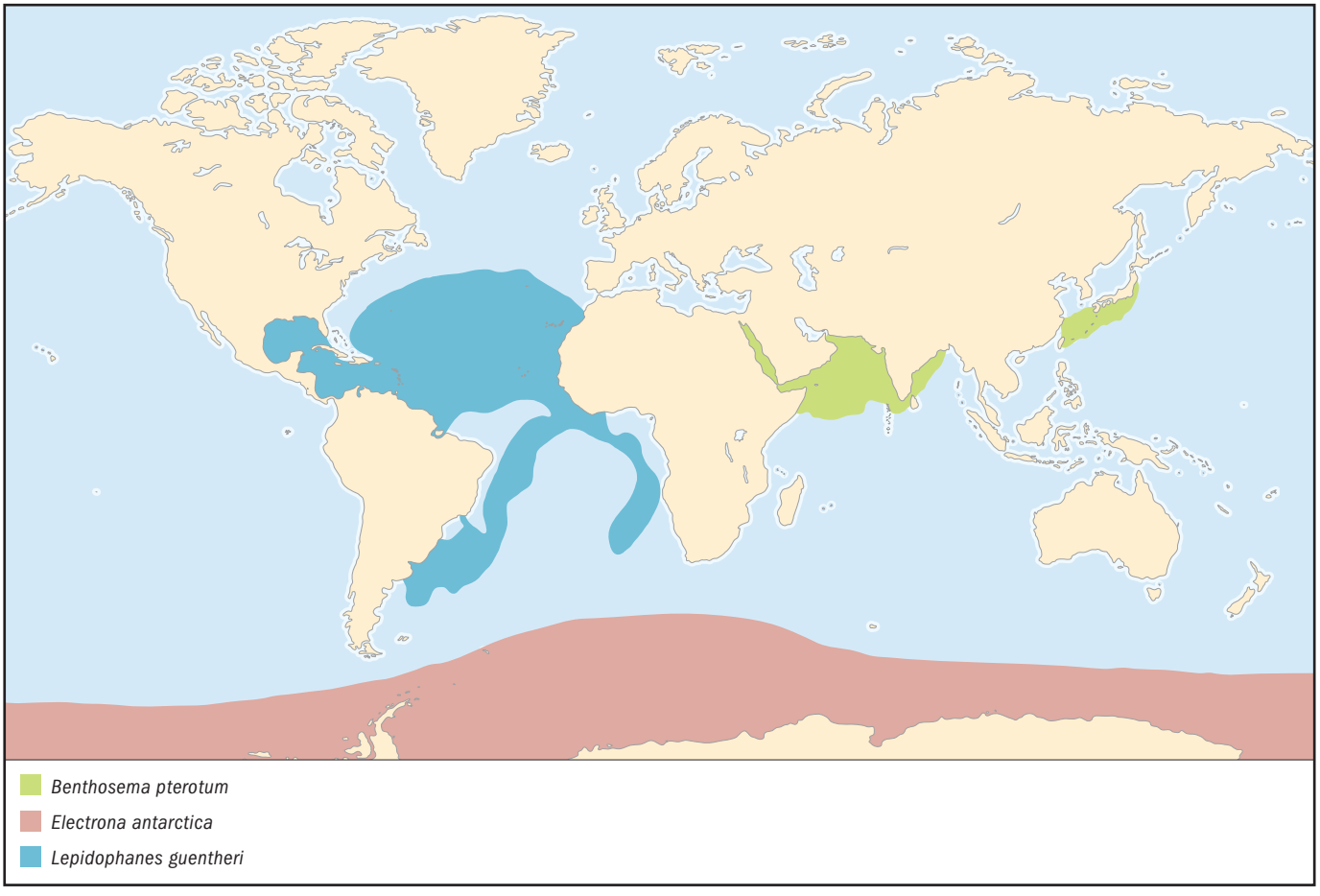
PHYSICAL CHARACTERISTICS
Deep, slightly pointed head with very large eyes. Pectoral fins are moderately long, reaching to about the middle of the dorsal fin. This is one of the smaller species of lanternfishes, reaching a maximum of 2 in (50 mm) SL, although relatively few specimens of greater than 1.6 in (40 mm) have been reported. Coloration is highly reflective silver on sides and ventral surfaces, with a blue-black dorsal surface.


Benthosema pterotum

DISTRIBUTION
Found primarily in the northern Indo-Pacific region, although larval specimens have been reported in the south Atlantic off South Africa. There are also some reported specimens from the eastern Pacific near Costa Rica and El Salvador as well. It is especially abundant in the northern Indian Ocean and Arabian Sea, and is the only myctophid species captured in the Gulfs of Aden and Oman.

HABITAT
Oceanic, mesopelagic. It is often reported to be associated with continental shelf edges and around islands. Some studies have suggested that it is benthopelagic. Reported daytime depth ranges are between 426 and 1,640 ft (130 and 500 m), with night depth ranges from the surface to about 984 ft (300 m).

BEHAVIOR
This species is a vertical migrator. It also is known to form extremely dense aggregations. Catch rates using large commercial pelagic fishing trawls have captured as much as 88 tons



(80 metric tons) per hour of fish in the northern Arabian Sea, where this species is especially abundant.

FEEDING ECOLOGY AND DIET
Crustacean zooplankton, especially copepods. There is a shift towards larger crustacean prey as the fish grow larger. Feeding occurs at night.

REPRODUCTIVE BIOLOGY
Sexes are separate and dimorphic. Like other members of this genus, sexually mature males have a series of luminescent scales in a supracaudal position, whereas in females, the luminescent scales are infracaudal. Sexual maturity in females occurs at around 1 in (25.4 mm) SL. Release of eggs and sperm is external, and reproduction occurs in the late afternoon and evening as the animals are migrating upwards; the buoyant eggs then float into the food-rich zone while developing. *Benthosema pterotum* is a serial batch spawner, releasing from 200 to 3,000 eggs per batch, depending on body size. Spawning appears to continue from the onset of sexual maturity until death, with an estimated life span of slightly less than one year.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Benthosema pterotum is a target species for commercial capture by Iran. Plans were to use a processing vessel of 165 tons (150 metric tons)/day processing capacity to convert *B. pterotum* captured in the Gulf of Oman (a region of especially high density for this species) into fish meal for fertilizer. It is unknown whether these operations are still continuing. ◆

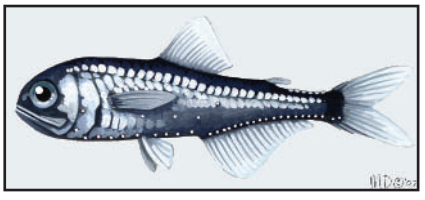
No common name
Electrona antarctica

FAMILY
Myctophidae

TAXONOMY
Scopelus antarcticus Günther, 1878, Antarctic Ocean, Stations 156 and 157.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The species is characterized by a relatively large, deep head, with large eyes, and a long series of photophores above the anal fin. Pectoral fins are moderately long, reaching to about the middle of the dorsal fin. It is a large species, attaining a maximum reported size of more than 4 in (101.6 mm) SL. Sides and ventral surfaces are highly reflective and silver in color, with a deep blue-black along the dorsal surface.


Electrona antarctica

DISTRIBUTION
Considered to be endemic to Antarctic waters, although some small individuals, thought to be waifs, have been collected north of the Antarctic convergence. Considered one of the few truly polar species of myctophids.

HABITAT
Oceanic, mesopelagic. During daylight hours, this species resides below 1,640 to over 2,952 ft (500 to over 900 m) depth, while at night it can be found between 0 and 990 ft (0 and 300 m). During periods of 24-hour sunlight, "nighttime" depths of capture usually are more than 660 ft (200 m).

BEHAVIOR
The species is a strong vertical migrator, and is known to enter the very surface waters during night hours, where it is often eaten by seabirds.

FEEDING ECOLOGY AND DIET
This species is a crustacean zooplanktivore. It feeds on copepods, ostracods, and euphausiids. Larger individuals are known to have a greater incidence of euphausiids in their diet, especially the abundant krill, *Euphausia superba*.

REPRODUCTIVE BIOLOGY
Sexes are separate, and males are distinctly smaller than females at a maximum size of 3.3 in (83.8 mm), vs. 4 in (101.6 mm) SL. Although age has been estimated to be as much as 11 years, the most reliable report has suggested a maximum age of 3.5 years for this species. It is believed to attain sexual maturity in its second year. Based on the staging of oocytes in collected females, it is thought that this species has a restricted spawning period during the southern spring.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Of no known commercial use, but is an important link in southern ocean ecosystem dynamics. ◆

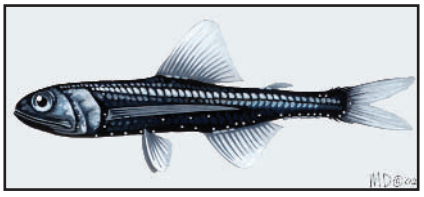
No common name
Lepidophanes guentheri

FAMILY
Myctophidae

TAXONOMY
Lampanyctus güntheri Goode and Bean, 1896, based on single specimen "obtained by the Gloucester fleet."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Males and females both exhibit elongated, slender bodies with relatively pointed heads. Maximum length is about 2.75 in (69.9 mm) SL. There is no apparent sexual dimorphism. In addition to body photophores, numerous luminescent scales are found along the bases of the dorsal, anal, and adipose fins, plus along the ventral region of the tail. A distinctive feature of this species is the length of the pectoral fins, which are very long, extending to the posterior


Lepidophanes guentheri

end of the anal fin. Freshly preserved specimens are deep blue-black along the dorsal surface and iridescent silver along the sides and ventral region.

DISTRIBUTION
Confined to the Atlantic Ocean. It is one of the most abundant myctophid species in the Gulf of Mexico, and according to the comprehensive zoogeographic analysis of Atlantic myctophids by Backus et al. (1977), it is "… the ranking myctophid in the Atlantic Tropical Region."

HABITAT
Oceanic, mesopelagic. *Lepidophanes guentheri* has been reported between 1,394 and 2,460 ft (425 and 750 m) during the day and between 131 to 410 ft (40 and 125 m) at night in the tropics, but at higher latitudes (off Bermuda and in the Gulf of Mexico), its daytime and nighttime depths are usually deeper (2,296–3,300 ft, or 700–1,000 m during the day; 165–574 ft, or 50–175 m, at night). A detailed study on the Gulf of Mexico population reported nonmigration by juveniles.

BEHAVIOR
Throughout its range in tropical environments, this species is a dominant component of the vertically migrating mesopelagic fauna. No other specifics of behavior are available.

FEEDING ECOLOGY AND DIET
This species is a crustacean zooplanktivore. Primary prey are copepods and at larger sizes, euphausiids. In a detailed study conducted in the eastern Gulf of Mexico, this species was one of three myctophid species that were found to remove more than 10% of the zooplankton biomass in epipelagic waters at night.

REPRODUCTIVE BIOLOGY
Males and females are separate sexes, or dioecious. This species is a serial batch spawner, releasing from 600 to more than 2,000 eggs per batch, depending on fish size. Sexual maturity in females is attained between 1.6 and 1.8 in (40.6 and 45.7 mm) SL. Eggs are released at night when the adults are at their shallow nighttime depths. Once sexual maturity is attained, spawning is repeated continuously every few days until death. Maximum age for this species has been shown to be about 14 months in the Gulf of Mexico.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

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John V. Gartner Jr., PhD

Lampridiformes
(Opah and relatives)

Class Actinopterygii
Order Lampridiformes
Number of families 7

Photo: The oarfish (*Regalecus glesne*) is a deep sea dweller and rarely seen alive. (Photo by Robert E. Pelham. Bruce Coleman, Inc. Reproduced by permission.)

Evolution and systematics

The order Lampridiformes contains some of the most uniquely evolved, morphologically diverse, and colorful forms of living fishes. The imaginative common names of these species (oarfish, ribbonfish, tube-eye, inkfish, and unicornfish), their extreme rarity, and their fanciful reputations combine to promote the assemblage as subjects of public curiosity. In turn, scientists have particular interest in the group, because its members include species that are basal sister taxa in phylogenetic analysis of higher perchlike fishes and because many lampridiform species have evolved highly specialized traits. The icon of the order, *Regalecus glesne*, is a fabled species whose tremendous length (up to 55 ft, or 17 m—the longest of all bony fishes), bright crimson fins, long dorsal rays, silvery form, and tendency to appear suddenly at the ocean surface after wind storms brought fearful cries of "sea monster!" from ancient mariners. Recently, living oarfish have been sighted and filmed by divers in the clear waters of the Caribbean, and these accounts have stirred considerable popular interest. The order includes the deep-bodied *Lampris guttatus*, a brightly colored and heavy species (up to 600 lb, or 275 kg) that brings good prices in commercial markets, as well as other, lesser known and much smaller species that are never seen by the public and only infrequently collected on scientific expeditions.

In all, the order Lampridiformes (formerly known as the Allotriognatha) comprises 21 extant species classified in 12 genera and seven families. Skeletal evidence of another six or so extinct species has been found in fossil beds around the world. The current lampridiform classification is as follows: family Veliferidae, with two monotypic genera (containing one species), *Velifer* and *Metavelifer*; family Lamprididae, with one genus, *Lampris* (two species); family Stylephoridae, with one monotypic genus, *Stylephorus*; family Radiicephalidae, with one monotypic genus, *Radiicephalus*; family Lophotidae, with two monotypic genera, *Lophotus* and *Eumecichthys*; family Trachipteridae, with three genera, *Trachipterus* (four species), *Zu* (two species), and *Desmodema* (two species); and family Regalecidae, with two monotypic genera, *Regalecus* and *Agrostichthys*.

The oarfish and its relatives form a natural assemblage of fishes that evolved from a common *Velifer*-like ancestor sometime in the late Cretaceous or early Eocene. Independent investigations of lampridiform evolution, one using only morphological characters and another using both morphological and molecular characters in a total-evidence analysis, agree on the following shorthand pattern of phylogenetic relationships of lampridiform families: Veliferidae (Lampridae (Stylephoridae ((Lophotidae + Radiicephailidae) (Regalecidae + Trachipteridae)))). In this shorthand scheme, sequentially, the taxon on the left and outside the parentheses is the sistergroup to the taxa within the parentheses. Thus, Veliferidae is the sistergroup to Lampididae plus all other lampridiforms. Likewise, Lampididae is the sistergroup to Stlylephoridae and all other lampridiforms. Finally, Stylephoridae is the sistergroup to two clades, each containing two families. To date, there have been no phylogenetic studies of species-level relationships, and, in some families, species-level and genera-level revisions are required.

Until recently, the limits of Lampridiformes and the systematic position of the order within the larger context of other bony fishes have been difficult, unresolved issues. Some scientists have provisionally included other families of deep-sea fishes (e.g., Ateleopodidae, Mirapinnidae, and Megalomycteridae) in Lampridiformes, but recent phylogenetic analysis confirms that these additional families are unrelated. Lampridiform fishes lack certain specializations of the axial skeleton (principally, patterns of small bones and ligaments

The oarfish (*Regalecus glesne*) is a long serpent-like fish that was thought to be a sea serpent 100 years ago. It becomes disoriented in rough seas and may writhe around on the surface. (Illustration by Wendy Baker)

associated with anterior vertebrae) that characterize more advanced fishes. These higher taxa, collectively classified as the Acanthomorpha, include the beardfish (*Polymixia*) and numerous major categories, including the codlike fishes (Paracanthopterygii) and perchlike fishes (Perciformes). Otherwise, Lampridiformes possess many other acanthomorph traits. Thus, the order Lampridiformes is considered the primitive sister taxon to all higher fishes, a significant group making up approximately 60% of all known teleost species. This systematic position makes the order, especially its basal members, veliferid lampridiforms, important to scientists hoping to unravel the intricate evolutionary histories of the diverse assemblage of acanthomorph fishes.

Abrupt transitions from shallow, nearshore habitats to the open ocean and from deep-bodied (termed bathysomous forms) to elongate (taeniosomous) forms are two major events hypothesized to have shaped the evolution of Lampridiformes. The basal and most generalized lampridiform family is the Veliferidae, moderate-sized, shallow-dwelling fishes that reside in coastal seas. All other lampridiforms are open-ocean, epipelagic or mesopelagic fishes. Since veliferids are the basal sister group to the Lamprididae (plus all other lampridiforms), it appears that an early important event in the evolution of the lampridiform lineage was the invasion and subsequent adaptation of veliferid-like progeny to pelagic life in the deep ocean. *Lampris*, a ponderous and deep-bodied species, is the sister group to the tube-eyes (Stylephoridae) and all other lampridiforms. The second significant evolutionary transition occurs at this level in the phyletic sequence, because tube-eyes and their relatives are all slender, elongate, ribbon-shaped species. As the most highly evolved taxa of the order, *Stylephorus* is the sister taxon to two distinct clades in the lampridiform lineage, the inkfishes (represented by Lophotidae and Radiicephalidae) and the oarfishes and ribbonfishes (Regalecidae and Trachipteridae).

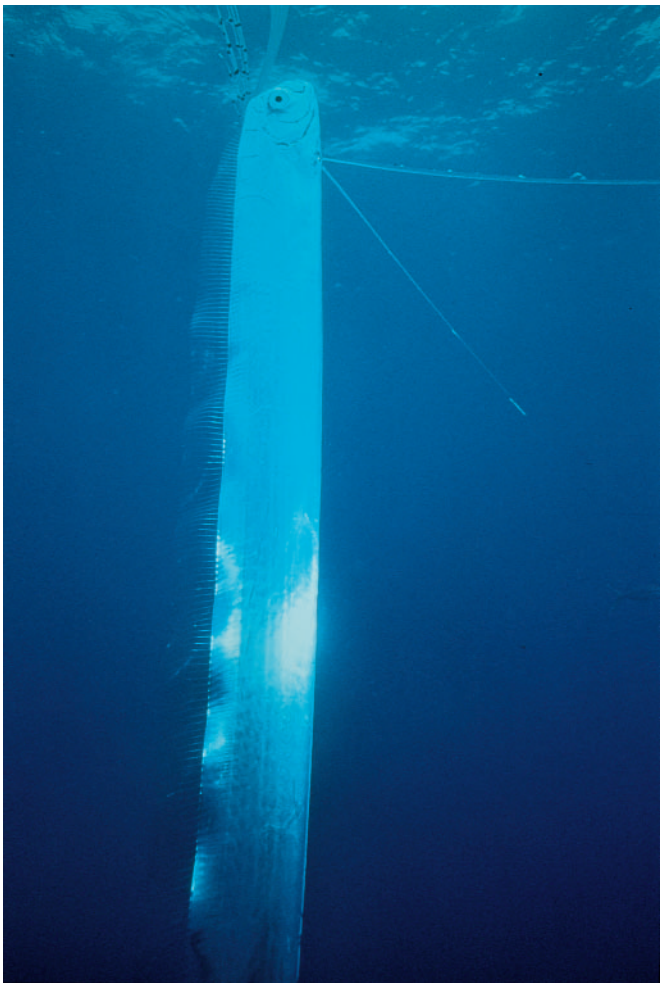
Numerous fossil forms have been attributed to lampridiform ancestry, some of which may be incorrectly classified. The oldest known lampridiform fish is *Nardovelifer altipinnis*, a recently described fossil found in Cretaceous deposits of Nardo near Lecce, in southern Italy. Eocene deposits near Verona, Italy, have yielded two species, *Veronavelifer* and *Bajaichthys*. Additional fossil taxa include several very large (up to 10 ft, or 3 m, in length) *Lampris*-like species discovered in Miocene deposits in California (*Lampris zatima*) and Oligocene deposits in New Zealand (an new, unnamed taxon) as well as two Oligocene lophotids, *Protomecicthys* and *Protolophotus*.

Physical characteristics

Unlike all other teleostean fishes, lampridiforms lack a ligamentous connection between the bones of the upper jaws (maxillae) and the cheekbones. In addition, the nasal cartilage that partially supports the maxillae is large and inserted in a groove on the skull in the frontal region. These two features allow the upper jaws of lampridiforms to be carried far forward during feeding, a modification that results in extreme jaw protrusion and expansion. In one species, *Stylephorus chordatus*, jaw protrusion allows the mouth cavity to expand suddenly to 40 times that of the closed mouth and permits *Stylephorus* to capture small planktonic prey items with considerable suction. Other unique physical characteristics of the order include crimson red fins, brightly colored bodies, and anterior placement of the thin bones (pterygiophores) that support the first dorsal fin. The elongate forms possess 60–150 vertebrae, whereas veliferids and lampridids have 33–46 vertebrae.

Distribution

Examples of most lampridiform families are rarely seen alive, and distribution records usually result from dead or dying animals that become stranded on beaches or are observed injured or disoriented at the sea surface. Some small species have been taken in scientific expeditions using midwater trawls. One species in the family Veliferidae inhabits shallow, nearshore waters of the Indian and Pacific Oceans. Another veliferid has been taken in bottom trawls on Pacific continental slopes and sea mounts. The remaining lampridiform families contain mesopelagic and epipelagic species that are distributed widely in temperate, subtropical, and tropical regions of all oceans except polar seas. Some species in the family Trachipteridae have somewhat restricted ranges. Radiicephalids have been collected only in the Atlantic Ocean and are extremely rare. One species of the family Lampididae, the rare southern opah, occurs around the world in the subantarctic zone below 45° south latitude.



Thirteen feet (4 m) in length with pelvic and anterior dorsal-fin rays extended, an oarfish (*Regalecus glesne*) rises from the deep ocean to sunlit surface waters in the Bahamas. The elongate rays bear fleshy, pigmented swellings but this specimen lacks the bright, crimson red fins that are typical of lampridiform fishes. (Photograph by Brian J. Skerry; National Geographic Society. Reproduced by permission.)

Habitat

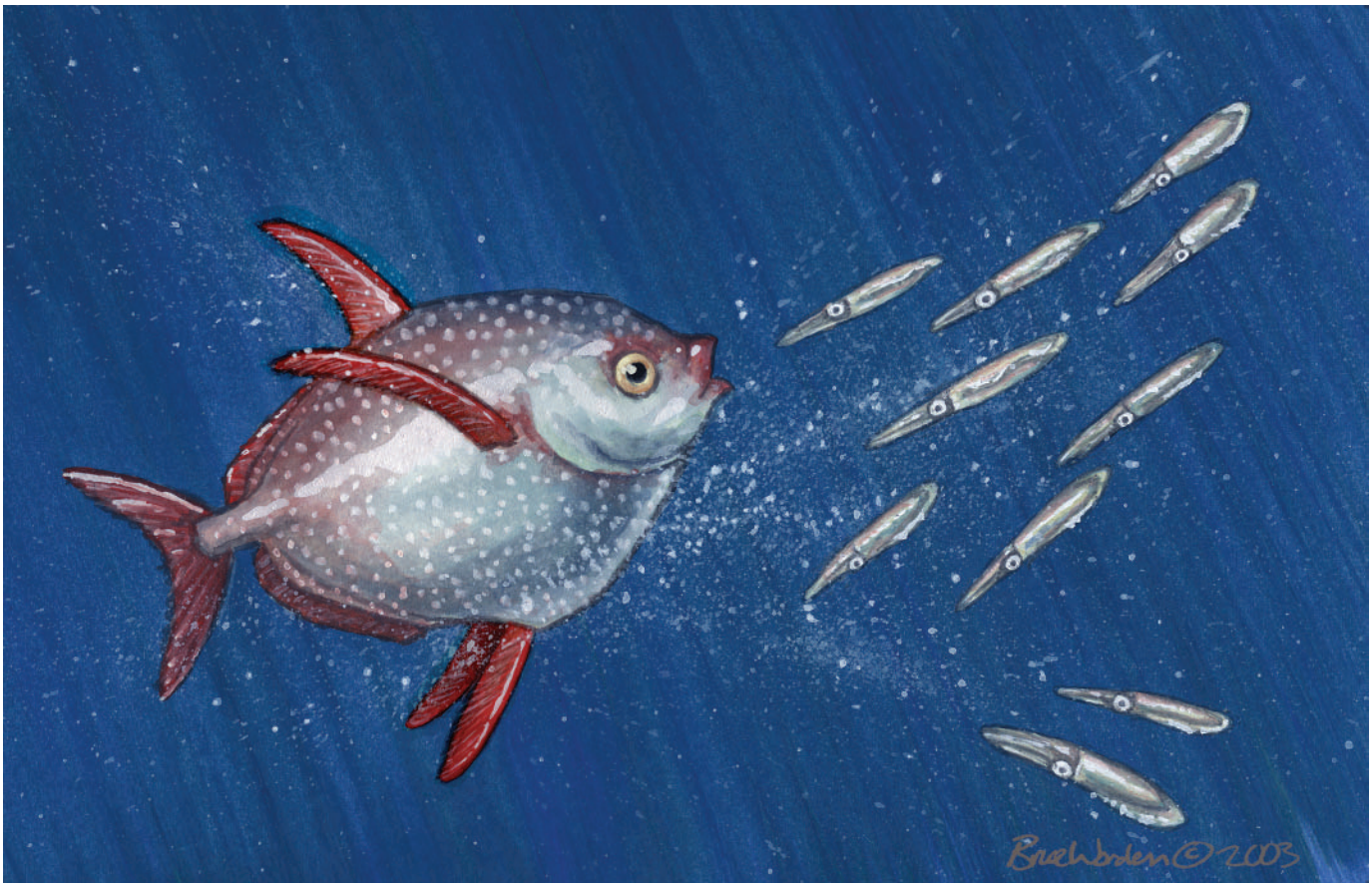
Lampridiforms are strictly marine fishes. Veliferids occur at depths of 130–360 ft (40–110 m) in nearshore regions. *Lampris* occasionally is taken near the surface in hook-and-line fisheries off the California coast but also is known from deeper waters. Other lampridiform fishes inhabit the deep ocean, from surface waters to depths of hundreds of feet. Very little is known about the specific habitats of these species or their associations in pelagic communities.

Behavior

Observations of living specimens are extremely limited. Submersible sightings and diver observations suggest that elongate forms, such as *Regalecus* and trachipterids, normally orient in a vertical, head-up position and move vertically in the water column by undulating their long fin bases. In a short video of an oarfish sighted near the Bahamas, the specimen hovered almost motionless near the surface and then descended vertically and rapidly out of sight when disturbed by divers. Veliferids and lampridids swim horizontally in a typical teleost posture. Lampridids are powerful swimmers, using large pectoral fins for forward propulsion. Lampridiform fishes probably do not exhibit schooling behavior—all sightings and strandings have been of individuals. Feeding and spawning have never been observed. One regalecid, *Agrostichthys parkeri*, has been reported to deliver a mild electric shock when handled. *Lophotus* and *Radiicephalus* have specialized organs that empty into the cloaca and expel large quantities of a dark, squidlike ink when disturbed.

Feeding ecology and diet

Lampridiform fishes consume small planktonic crustaceans, especially euphausids; small to moderate-sized squids; and small to medium-sized fishes. These data come from anecdotal observations made of the stomach contents of single specimens. There have been no detailed studies of the feeding ecology of any lampridiform species. Very little is



An opah (*Lampris guttatus*) hunts squid. (Illustration by Bruce Worden)

known about predators of lampridiform fishes. Some species have been found in the stomachs of tunas.

Reproductive biology

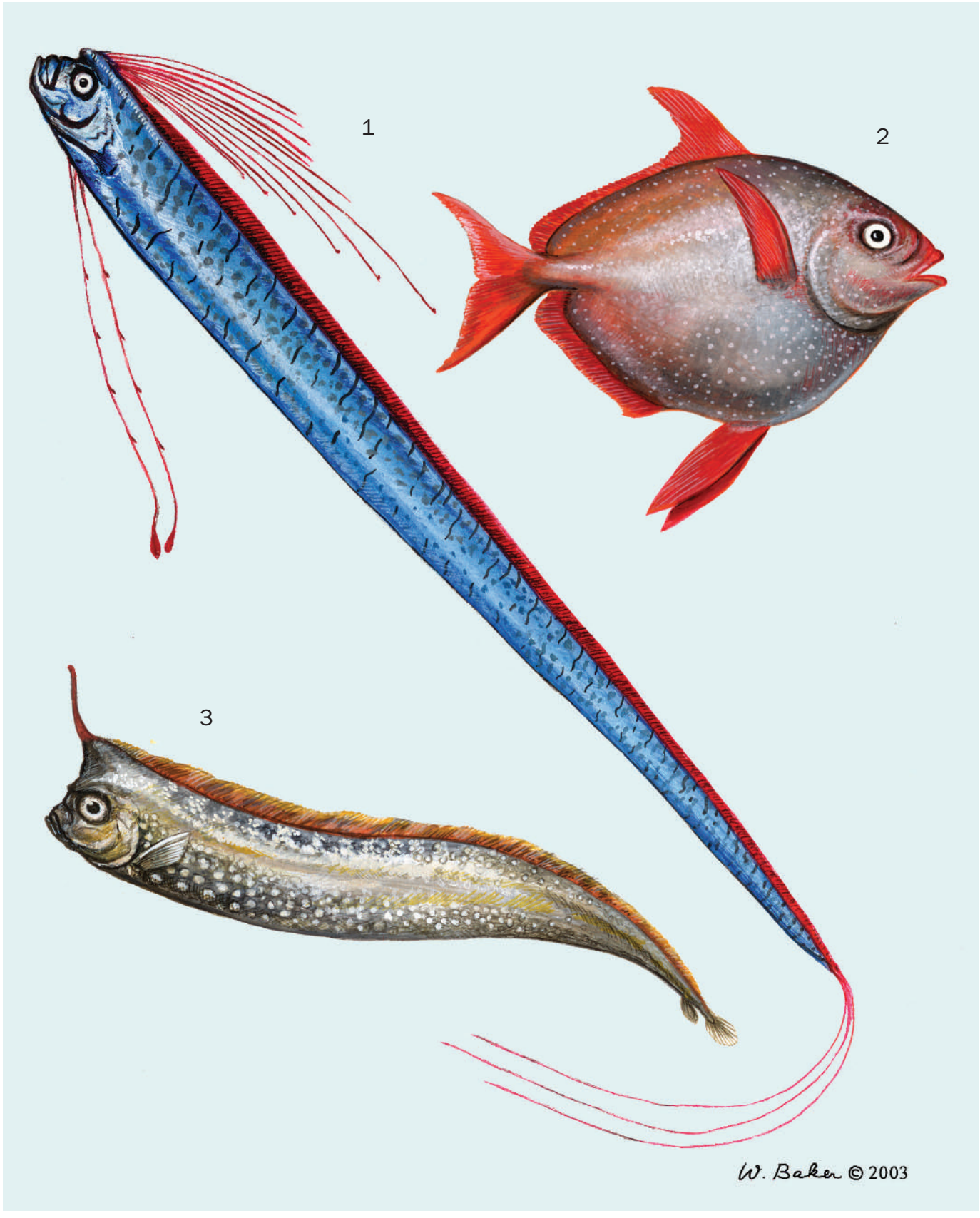
Spawning has not been observed, but lampridiform fishes probably are broadcast spawners, because eggs are planktonic and have been identified for many lampridiform species in scientific collections. Eggs are large, 0.08–0.24 in (2–6 mm) in diameter, and brightly colored, usually in hues of red, pink, or amber. Incubation takes place in surface waters for approximately three weeks. At hatching, larvae have fully developed mouths and digestive tracts and begin to feed immediately on minute plankton. Larval lampridiforms are distinguished further by long, ornamented dorsal and pelvic rays. Some species, especially trachipterids, undergo abrupt metamorphosis from the larval to the juvenile form.

Conservation status

No lampridiform species are listed by the IUCN, but all are very rare. Care should be taken to ensure conservation of veliferid lampridiforms, because of their unique role in phylogenetic studies as basal taxa.

Significance to humans

Lampridiform fishes, especially the large, elongate species, attract considerable public attention when they are stranded or beached, owing to their rarity and unusual morphological features. *Lampris guttatus* has excellent flesh and is prized as bycatch of certain offshore fisheries. Most other lampridiform fishes are considered inedible by those who have recorded attempts to eat them.



1. Oarfish (*Regalecus glesne*); 2. Opah (*Lampris guttatus*); 3. Crestfish (*Lophotus lacepede*). (Illustration by Wendy Baker)

Species accounts

Opah
Lampris guttatus

FAMILY
Lampridae

TAXONOMY
Lampris guttatus Brunnich, 1788, North Sea.

OTHER COMMON NAMES
English: Moonfish, Jerusalem haddock.

PHYSICAL CHARACTERISTICS
Large, oval, colorful species with silvery blue, iridescent body; bright red fins and snout; large eyes; and white spots covering the body and the bases of the dorsal, anal, pelvic, and caudal fins. Length typically 3.3 ft (1 m) and total weight approximately 600 lb (275 kg). Pectoral fins large and horizontally oriented. The dorsal and anal fins have elongate anterior portions, and the caudal fin is moderately forked. Superficially resembles the ocean sunfish, *Mola mola*, a pelagic species that is similarly large and somewhat oval but not colorful and lacks pelvic fins and a caudal fin.

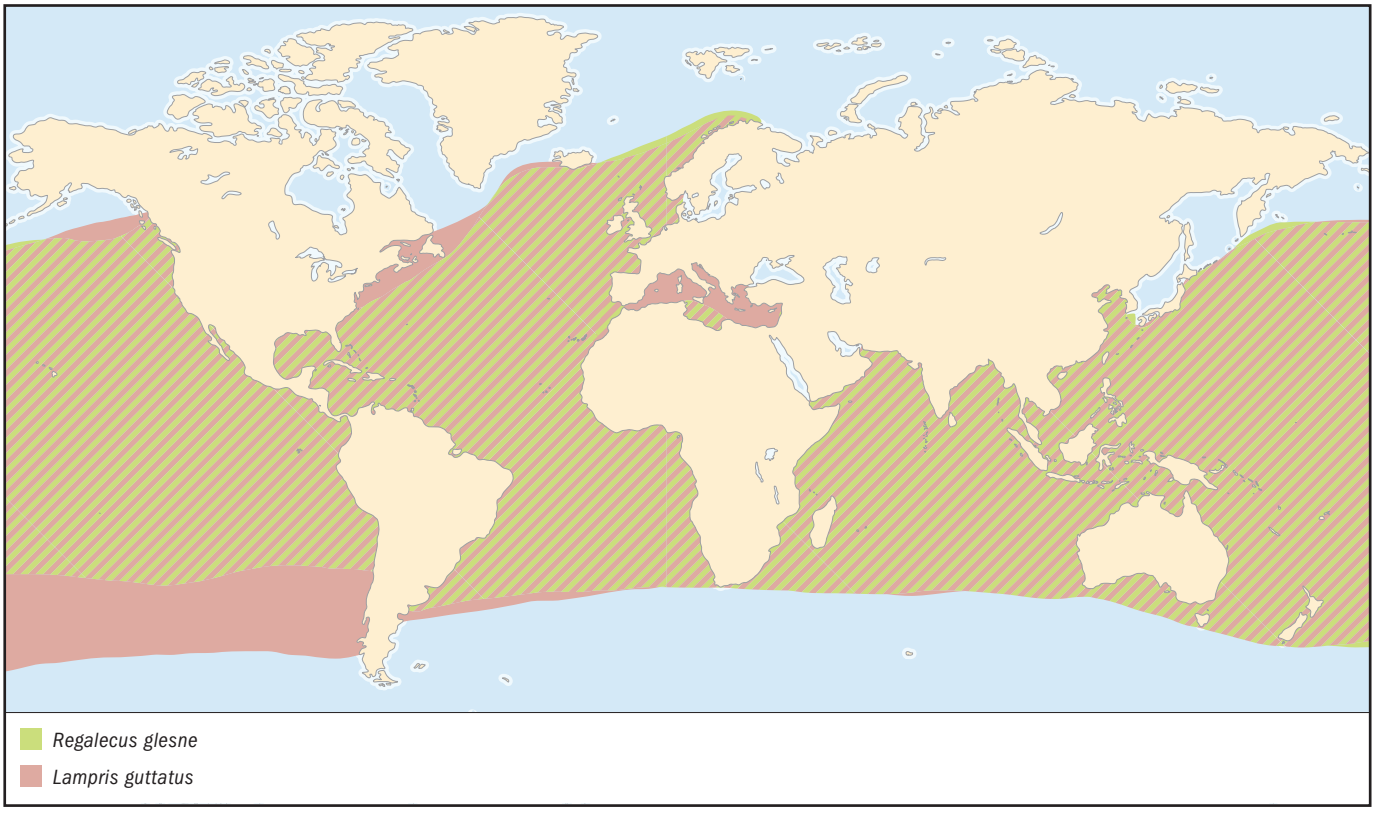
DISTRIBUTION
All oceans, including the Mediterranean Sea, but not polar oceans. Most distribution records come from catches of pelagic longline gear set for tuna and swordfish.

HABITAT
Lower epipelagic zone, generally in surface waters to perhaps 1,640 ft (500 m). Analysis of data from Japanese longline fisheries shows that catches of opah increase with depth to about 920 ft (280 m) in the central and eastern Pacific Ocean.

BEHAVIOR
There are no published observations of living *Lampris*. Swimming behavior has been inferred from the anatomical and morphological features of the pectoral fin. The massive shoulder girdle; the presence of extensive pectoral musculature, including a large red muscle mass; and the horizontal placement of the pectoral fin base suggest that the opah swims by pectoral-fin "flapping." This unusual swimming mode apparently allows the opah to swim rapidly, since it is an effective predator of active prey. Records of occurrence of opah are sporadic and widespread, suggesting that the species is a solitary wanderer in the world's oceans.

FEEDING ECOLOGY AND DIET
Predatory species that consumes squids and octopus as well as small to medium-sized fishes. Fish species eaten include hake, rockfish (Scorpaenidae), ophidiiforms, small dolphins (*Coryphaena* species), berycoids, argentines, and other mesopelagic species. There is one unusual report of opah feeding on small clams in shallow waters off Florida. Opah take live and cut bait on hooks as well as trolled fishing lures off the California coast. Opah can consume large quantities of prey. The stomach of one 126-lb (57-kg) specimen was found to contain 63 fishes, 8 cephalopods, and 7 crabs.

REPRODUCTIVE BIOLOGY
Little is known of the spawning behavior, spawning seasons, or spawning habitats of *Lampris*. Advanced-stage oocytes removed



from the ovaries of ripe fish have a thick shell (chorion) that is amber to pink in color. Fertilized eggs are probably free floating but have not been identified in plankton collections. Only a few larval examples have been collected, all in the Atlantic Ocean. Larvae are slender and somewhat elongate initially but rapidly become deep-bodied. Pigment is confined to the head region and above the gut in the smallest specimens, but larger larvae have extensive scattered melanophores (pigmented cells) covering the entire body except the fins. The anterior rays of the dorsal and pelvic fins are elongate. Rates of mortality and growth, feeding habits, and predators of larvae are largely unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The species is a marketable bycatch of longline fisheries and is pursued by recreational anglers. The all-tackle game fish record is 162.9 lb (73.9 kg), and this specimen was captured off California in 1998. Its flesh is considered good, and it is thought to be excellent as a smoked product. ◆

Crestfish
Lophotus lacepede

FAMILY
Lophotidae

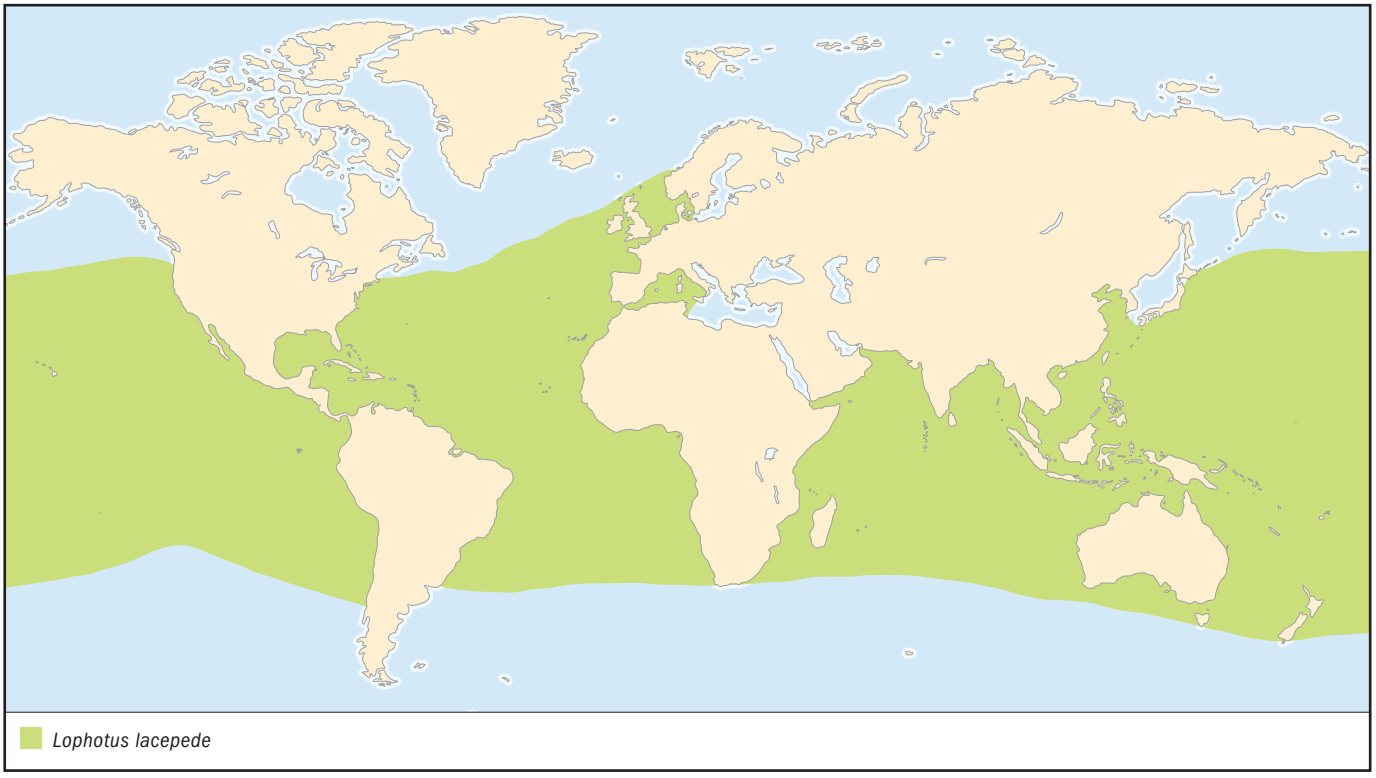
TAXONOMY
Lophotus lacepede Giorna, 1809, type locality unknown.

The taxonomy of *Lophotus* is confused, and the genus is in need of revision. There is probably only one widely distributed species, but a number of nominal forms exist (*L. cepedianus*, *L. capellei*, and *L. cristatus*), all of which may be synonyms of *L. lacepede*.

OTHER COMMON NAMES
English: Highbrow crestfish, inkfish, crested oarfish.

PHYSICAL CHARACTERISTICS
The supraoccipital (a cranial bone situated above the eye) of *L. lacepede* bears a strong and enlarged anterior process that projects anteriorly over the forehead. This skeletal feature also is strongly developed in the crestfish's closest relative, *Eumecichthys fiski*, the unicornfish. The anterior process lies directly beneath the anterior dorsal fin rays and supports a large fleshy protuberance (the crest or horn) that gives the forehead of these fishes their distinct appearance. In *L. lacepede* the crest is thick and deep, and the forehead is either blunt or slightly projecting. In the unicornfish the fleshy protuberance is slender and greatly elongate, forming a long horn on the forehead. The body of *L. lacepede* is relatively long, attaining a total length of about 4.9–6.6 ft (1.5–2.0 m) and ribbon-like. Fresh specimens have been described as blackish blue, light brown, or silvery, sometimes with scattered white spots. Fins red. Dorsal fin extends the full length of the body. Caudal fin small and rounded. Pectoral fin low on body. Pelvic fins minute and located posterior to the pectoral fins. Anal fin small and located posteriorly. Possesses an elongate organ that lies above the lower intestine and produces thick, black, squidlike ink that is discharged through the cloaca. The unicornfish apparently does not possess this trait, although the ink gland is found in another lampridiform fish that is related closely to the lophotids, *Radiicephalus elongatus*.

DISTRIBUTION
Distributed widely in warm waters of all oceans. Specimens are rare, and most either have come from research cruises or have



been captured close to shore as stranded individuals in weakened condition.

HABITAT
Very little is known of the habitats of these fishes, owing to their rarity. Crestfish are apparently members of the epipelagic community and have been collected in surface waters to depths of only a few hundred feet (or meters). Some specimens have been taken in very shallow water, but they were probably dying.

BEHAVIOR
Almost nothing is known of the natural behavior of this species. Crestfish probably discharge ink when frightened. A large adult specimen captured and gaffed during a research cruise expelled a copious amount of ink. Crestfish may develop this capability at a young age, since late-stage larvae possess the ink gland.

FEEDING ECOLOGY AND DIET
Apparently consume small fishes, squid, and pelagic octopus.

REPRODUCTIVE BIOLOGY
Little is known of the spawning behavior, spawning seasons, or spawning habitats of *Lophotus* or its relatives. Eggs are pelagic and have been described from plankton collections in the Mediterranean Sea as relatively large, about 0.01 in (2.5 mm) in diameter, with many tiny spines covering the chorion. Early larvae have elongate dorsal and pelvic rays that bear large pigmented swellings. These rays often are damaged in capture and are absent in preserved specimens. Late larvae are sparsely pigmented and possess the internal ink gland, with the dark contents visible through the body wall. Vital rates, feeding habits, and predators of larvae are largely unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Oarfish
Regalecus glesne

FAMILY
Regalecidae

TAXONOMY
Regalecus glesne Ascanius, 1772. Most ichthyologists recognize a single species with worldwide distribution, but there are several nominal species that may be valid.

OTHER COMMON NAMES
English: King of the herrings.

PHYSICAL CHARACTERISTICS
Spectacular animals with long, slender, usually silver bodies; brillant red fins; a large, cockscomb-like plume of 6–10 anterior dorsal-fin rays; and long pelvic fins. When not damaged, the pelvic ray bears a large red swelling at its tip, from which its name is derived. Often attaining a length of 26–33 ft (8–10 m), oarfish are the longest of all bony fishes. (There are unconfirmed reports of some specimens reaching 56 ft, or 17 m.) The long body gradually tapers to a point. The caudal fin (when present and not damaged) is tiny, and its rays bear small, laterally projecting spinules. No anal fin. About 400 dorsal fin rays and 150 vertebrae. Some confusion exists concerning the distinction between regalecids and their close relatives, the trachipterids or ribbonfishes. Fishes in both families are elongate, have crimson red fins, lack an anal fin, and possess laterally projecting, small spines on the individual rays of the caudal and pelvic fins. The oarfish attains a greater length, has only two pelvic rays (one very elongate and one small and splintlike) and a very elongate anterior dorsal fin, and is relatively slender. The trachipterids are shorter, have more than two pelvic rays (though pelvic rays are absent in one genus), lack the extremely elongate dorsal rays, are relatively deeper-bodied, and have small spines on the lateral-line scales.

DISTRIBUTION
All oceans, including the Mediterranean Sea, but not polar seas. Most distribution records result from strandings of weak or dying fish in shallow water, although some fish have been captured by trawl.

HABITAT
Epipelagic species, normally inhabiting surface waters to depths of about 656 ft (200 m). The species is capable of occupying greater depths, however. Little is known of its specific habitat requirements or associations.

BEHAVIOR
Recent sightings of live fish by divers confirm that swimming is not accomplished by rowing the pelvic fins, as one might suppose from the name oarfish. Instead, oarfish move in the water column by undulations of the dorsal fin. The natural body position is vertical, with the head up and dorsal fin rays and pelvic rays extended outward. The pelvic fin may have a sensory capability, allowing the oarfish to "taste" its surrounding habitat. Its close relative, *Agrostichthys parkeri*, has been reported to be electrogenic, delivering a mild shock when handled. It is unknown whether the oarfish shares this capability.

FEEDING ECOLOGY AND DIET
Apparently consumes planktonic crustaceans and small fishes, but little is known of its feeding ecology. The stomach of a 9.8-ft (3-m) oarfish stranded in shallow waters off California contained a large volume of krill (euphausids), numbering about 10,000 individuals.

REPRODUCTIVE BIOLOGY
The spawning of oarfish has not been observed, and little is known of its spawning habits or seasons. The ovaries of a dying female, about 9.8 ft (3 m) in length, that was cast ashore on the west coast of Florida weighed 3.1 lb (1.4 kg) and contained approximately 140,000 unspawned eggs, some of which were ovulated. The female was observed in March, along with other dead male fish, presumably following a spawning occurrence. Oarfish eggs are pelagic and have been identified in plankton collections in the Mediterranean Sea and the waters off New Zealand. Eggs are large, 0.08–0.16 in (2–4 mm) in diameter, with pink to red chorions, and they contain numerous scattered oil droplets. Researchers report that eggs can take up to three weeks to incubate and that the emerging larva is highly developed at hatching, with a functional mouth and gut, a pigmented eye, and long dorsal and pelvic fin rays. Young oarfish resemble adults in most details and have been captured on research cruises in the Atlantic and Pacific Oceans. Vital rates, feeding habits, and predators of larvae are largely unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sightings of the oarfish usually stir considerable public attention, but the species has no commercial value, and its flesh is reported to be unpalatable. ◆

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Second Edition
Volumes 4 & 5 • Fishes I & II

Michael Hutchins, Series Editor,
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Dennis A. Thoney and Paul V. Loiselle, Advisory Editors

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Second Edition

Volume 5
Fishes II

Dennis A. Thoney, Advisory Editor
Paul V. Loiselle, Advisory Editor
Neil Schlager, Editor

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Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E.O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa-regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in super markets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"-places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade-the hunting of endangered wild animals for large scale human consumption-is pushing many species, including our closest relatives, the gorillas, bonobos and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought

specialists from various disciplines to write the sections with which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 205 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Grzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909–1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series has been completely revised and updated for the first time in over 30 years. Gale expanded the series from 13 to 17 volumes, commissioned new color paintings, and updated the information so as to make the set easier to use. The order of revisions is:

Volumes 8–11: Birds I–IV
Volume 6: Amphibians
Volume 7: Reptiles
Volumes 4–5: Fishes I–II
Volumes 12–16: Mammals I–V
Volume 3: Insects
Volume 2: Protostomes
Volume 1: Lower Metazoans and Lesser Deuterostomes
Volume 17: Cumulative Index

Organized by taxonomy

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science in which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the lower metazoans and lesser deuterostomes, in volume 1, the series progresses through the more advanced classes, culminating with the mammals in volumes 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. In the case of the volumes on Fishes, introductory chapters describe general characteristics of fishes, followed by taxonomic chapters dedicated to order and, in a few cases, suborder. Readers should note that in a few instances, taxonomic groups have been split among more than one chapter. For example, the order Cypriniformes is split among two chapters, each covering particular families. Species accounts appear at the end of the taxonomic chapters. To help the reader grasp the scientific arrangement, order and suborder chapters have distinctive symbols:

● = Order Chapter
○ = Suborder Chapter

The order Perciformes, which has the greatest number of species by far of any fishes order—and in fact is the largest order of vertebrates—has been split into separate chapters based on suborder. Some of these suborder chapters are again divided into multiple chapters in an attempt to showcase the diversity of species within the group. For instance, the suborder Percoidei has been split among four chapters. Readers should note that here, as elsewhere, the text does not necessarily discuss every single family within the group; in the case of Percoidei, there are more than 70 families. Instead, the text highlights the best-known and most significant families and species within the group. Readers can find the complete list of families for every order in the "Fishes family list" in the back of each Fishes volume.

As chapters narrow in focus, they become more tightly formatted. Introductory chapters have a loose structure, reminiscent of the first edition. Chapters on orders and suborders are more tightly structured, following a prescribed format of standard rubrics that make information easy to find. These taxonomic chapters typically include:

- Scientific name of order or suborder
- Common name of order or suborder
- Class
- Order
- Number of families

Main chapter
- Evolution and systematics
- Physical characteristics
- Distribution
- Habitat
- Feeding ecology and diet
- Behavior
- Reproductive biology
- Conservation status
- Significance to humans

Species accounts
- Common name
- Scientific name

Family
Taxonomy
Other common names
Physical characteristics
Distribution
Habitat
Feeding ecology and diet
Behavior
Reproductive biology
Conservation status
Significance to humans
Resources
Books
Periodicals
Organizations
Other

Color graphics enhance understanding

Grzimek's features approximately 3,500 color photos, including nearly 250 in the Fishes volumes; 3,500 total color maps, including more than 200 in the Fishes volumes; and approximately 5,500 total color illustrations, including nearly 700 in the Fishes volumes. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges.

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal specimens from the University of Michigan Zoological Museum library. In addition to illustrations of species, *Grzimek's* features drawings that illustrate characteristic traits and behaviors.

About the contributors

All of the chapters were written by ichthyologists who are specialists on specific subjects and/or families. The volumes' subject advisors, Dennis A. Thoney and Paul V. Loiselle, reviewed the completed chapters to insure consistency and accuracy.

Standards employed

In preparing the volumes on Fishes, the editors relied primarily on the taxonomic structure outlined in *Fishes of the World*, 3rd edition, by Joseph S. Nelson (1994), with some modifications suggested by expert contributors for certain taxonomic groups based on more recent data. Systematics is a dynamic discipline in that new species are being discovered continuously, and new techniques (e.g., DNA sequencing) frequently result in changes in the hypothesized evolutionary relationships among various organisms. Consequently, controversy often exists regarding classification of a particular animal or group of animals; such differences are mentioned in the text.

Grzimek's has been designed with ready reference in mind, and the editors have standardized information wherever feasible. For ***Conservation Status,*** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN web page at <http://www.iucn.org/themes/ssc/redlists/categor.htm>.

In addition to IUCN ratings, chapters may contain other conservation information, such as a species' inclusion on one of three Convention on International Trade in Endangered Species (CITES) appendices. Adopted in 1975, CITES is a global treaty whose focus is the protection of plant and animal species from unregulated international trade.

In the Species accounts throughout the volume, the editors have attempted to provide common names not only in English but also in French, German, Spanish, and local dialects. Readers can find additional information on fishes species on the Fishbase Web site: <http://www.fishbase.org>.

Grzimek's provides the following standard information on lineage in the ***Taxonomy*** rubric of each Species account: [First described as] *Acipenser brevirostrum* [by] LeSueur, [in] 1818, [based on a specimen from] Delaware River, United States. The person's name and date refer to earliest identification of a species, although the species name may have changed since first identification. However, the entity of fish is the same.

Readers should note that within chapters, species accounts are organized alphabetically by family name and then alphabetically by scientific name. In each chapter, the list of species to be highlighted was chosen by the contributor in consultation with the appropriate subject advisor: Dennis A. Thoney, who specializes in marine fishes; and Paul V. Loiselle, who specializes in freshwater fishes.

Anatomical illustrations

While the encyclopedia attempts to minimize scientific jargon, readers will encounter numerous technical terms related to anatomy and physiology throughout the volume. To assist readers in placing physiological terms in their proper context, we have created a number of detailed anatomical drawings. These can be found on pages 6 and 7, and 15–27 in the "Structure and function" chapter. Readers are urged to make heavy use of these drawings. In addition, selected terms are defined in the ***Glossary*** at the back of the book.

Appendices and index

In addition to the main text and the aforementioned ***Glossary,*** the volume contains numerous other elements. ***For Further Reading*** directs readers to additional sources of information about fishes. Valuable contact information for ***Organizations*** is also included in an appendix. An exhaustive ***Fishes family list*** records all recognized families of fishes according to *Fishes of the World,* 3rd edition, by Joseph S. Nelson (1994). And a full-color ***Geologic time scale*** helps readers understand prehistoric time periods. Additionally, the volume contains a ***Subject index.***

Acknowledgements

Gale would like to thank several individuals for their important contributions to the volume. Dr. Dennis A. Thoney, subject advisor specializing in marine fishes, created the overall topic list for the volumes and suggested writers and reviewed chapters related to marine fishes. Dr. Paul V. Loiselle, subject advisor specializing in freshwater fishes, suggested writers and reviewed chapters related to freshwater fishes. Neil Schlager, project manager for the Fishes volumes, coordinated the writing and editing of the text. Finally, Dr. Michael Hutchins, chief consulting editor for the series, and Michael Souza, program assistant, Department of Conservation and Science at the American Zoo and Aquarium Association, provided valuable input and research support.

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Polymixiiformes
(Beardfishes)

Class Actinopterygii
Order Polymixiiformes
Number of families 1

Photo: Beardfish (*Polymixia berndti*) live in deep marine waters, at 60–1,706 ft (18–520 m). They are rarely seen alive. This specimen was found near Oahu. (Photo by John E. Randall. Reproduced by permission.)

Evolution and systematics

Beardfishes of the order Polymixiiformes comprise a single living family, Polymixiidae, containing one genus, *Polymixia*, and, according to the revisional study of Kotlyar (1993), ten species. These seemingly nondescript fishes have a remarkably checkered taxonomic history, and few fishes have been shifted back and forth in different phylogenetic schemes as have these poorly understood animals. Although most systematists agree that Polymixiiformes are basal acanthomorphs, their precise placement at the base of this huge radiation of spiny-rayed fishes remains a mystery. In view of the longstanding confusion regarding the phylogenetic position of beardfishes, it should be clear that the small size of the order is no indication of their evolutionary importance. Although the group is represented today by a single genus, the Polymixiiformes have a much more diverse fossil record, and at least two families, the Aipichthyidae and Polymixiidae, containing some six genera, are currently recognized.

Polymixiiforms appear first in the fossil record in the late Cretaceous period, some 95 million years ago, and have been viewed as being of considerable importance to our understanding of the spiny-rayed fishes and their evolution. In 1964 the noted British paleoichthyologist Colin Patterson reviewed polymixiiform fossil diversity and discussed the striking similarities between them and certain families of living perciforms such as carangids (jacks) and monodactylids (moonfishes). Whether these similarities reflect the common phenomenon of convergent evolution or are the result of recent common ancestry remains an open question. Whatever the case, such an ongoing confusion serves to highlight the importance of Polymixiiformes to our understanding of the evolution of spiny-rayed fishes.

Physical characteristics

Polymixia are rather deep-bodied fishes, with prominent blunt snouts and large eyes. Their dorsal and anal fins bear well-developed spines, but a spine is lacking in the subabdominally positioned pelvic fins, which have a single, segmented, leading ray and six branched rays. All beardfishes are characterized by the possession of a pair of hyoid barbels. These "chin" barbels are internally supported by three branchiostegal rays of the hyoid arch, and their characteristic appearance lends their bearers the name "beardfishes." A 2001 study by Kim and his colleagues highlights the unique nature of the anatomy and muscular control of beardfish barbels.

Distribution

Beardfishes are known to occur in the Atlantic, Indian and Western Pacific oceans, as well as in tropical and subtropical waters. Worldwide collection data for *Polymixia* species are poor, and sampling in many regions is limited or nonexistent. When caught, most species are taken at depths ranging from 492–2,132.5 ft (150–650 m), but catches from as shallow as 164 ft (50 m) have been recorded.

Habitat

Very little is known of the habitat preferences of *Polymixia* species, but the presence of chin barbels suggests a bottom-dwelling mode of life, probably over sandy or muddy substrates.

Behavior

Nothing is known.

Feeding ecology and diet

The stomach of *Polymixia* is thick walled and muscular, often with over 100 pyloric ceca (pouches). Analyses of the gut contents indicate an opportunistic diet of crustaceans, squid, and small fishes. Interestingly, beardfishes are recorded among the stomach contents of the Indian Ocean coelacanths, as well as in those of a wide range of other fish predators.

Reproductive biology

Polymixia eggs are unknown, and the smallest individual so far identified is a 0.15 in (0.39 cm) postflexion larva, which was described in some detail by Konishi and Okiyama, who noted the presence of moderately developed head spination similar to that found in many beryciform fishes. Reproductive biology is virtually unknown, but sexual dimorphism in coloration has been noted in *P. lowei*, where an intense black marking on the anal fin and both lobes of the tail fin are present only in male fish.

Conservation status

None of the *Polymixia* species are included on the IUCN Red List. Although catches of some species are relatively high in some regions, there are no indications of overfishing.

Significance to humans

Beardfishes are marketed for human consumption in most regions; however, commercial catches are limited but growing. As catches of other species have declined, a number of Pacific beardfish species have been tagged as having unexploited fisheries potential.

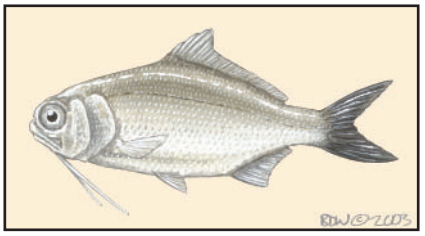
Species accounts

Stout beardfish
Polymixia nobilis

FAMILY
Polymixiidae

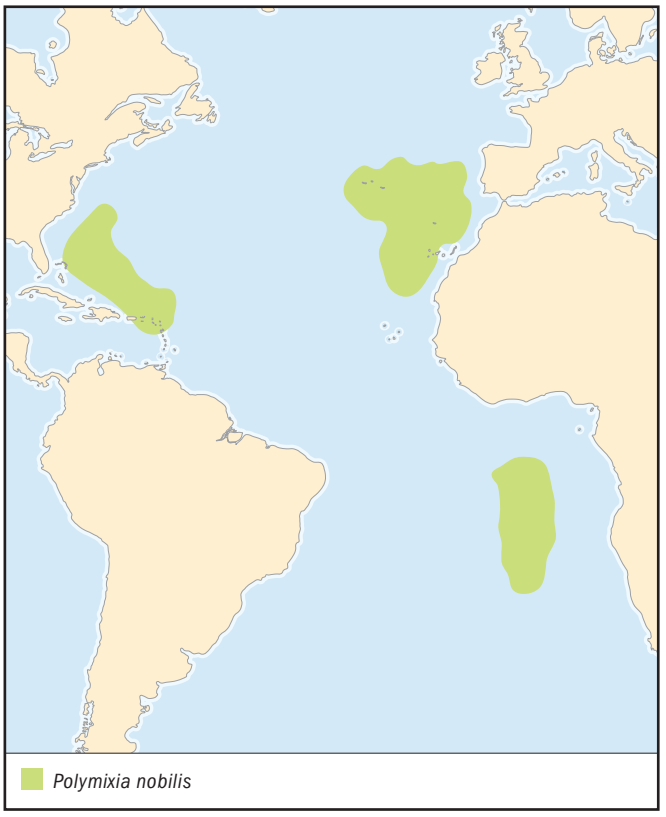
TAXONOMY
Polymixia nobilis Lowe, 1836, off Madeira.

OTHER COMMON NAMES
Portuguese: Salmonete do Alto.

PHYSICAL CHARACTERISTICS

Polymixia nobilis

Maximum length 19.6 in (50 cm). Deep-bodied, with a prominent blunt snout and large eyes. The ctenii on the scales are arranged in wedgelike rows, and the hyoid barbels are long and filamentous. Dark bronzy-grey dorsally and silvery ventrally.

DISTRIBUTION
Found only in Atlantic Ocean. In western Atlantic, they occur from Norfolk south to Lesser Antilles, Cuba, and Bahamas, where they are sympatric with *Polymixia lowei*. The stout beardfish is the only beardfish in the eastern Atlantic, where it occurs from the Azores and Canary Islands south to St. Helena. Records of *Polymixia nobilis* from the Pacific are now known to be misidentifications.



HABITAT
Semihard and soft bottoms on the continental shelf and slope.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Feeds on crustaceans, squid, and small fishes.

REPRODUCTIVE BIOLOGY
Eggs are unknown and reproductive biology is virtually unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Stout beardfishes are of some commercial importance, particularly in Madeira, where they are marketed fresh and frozen. ◆

Resources

Periodicals

Kim, B. J., M. Yabe, and K. Nakaya. "Barbels and Related Muscles in Mullidae (Perciformes) and Polymixiidae (Polymixiiformes)." *Ichthyological Research* 117 (2001): 409–413.

Konishi, Y., and M. Okiyama. "Morphological Development of Four Trachichthyoid Larvae (Pisces: Beryciformes), with Comments on Trachichthyoid Relationships." *Bulletin of Marine Science* 60 (1997): 66–88.

Kotlyar, A. N. "A New Species of the Genus *Polymixia* from the Kyushu-Palau Submarine Ridge and Notes on the Other Members of the Genus." *Journal of Ichthyology* 2 (1993): 30–49.Patterson, C. "A Review of Mesozoic Acanthopterygian Fishes, with Special Reference to Those of the English Chalk." *Philosophical Transactions of the Royal Society of London* 3 (1994): 213–482.

Other

"Coelacanths: Coelacanth Fact Sheet." South African Institute for Aquatic Biodiversity. Ichthos, 2001. (March 20, 2003). <http://www.saiab.ru.ac.za/educoel1.htm>

Melanie Stiassny, PhD

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Percopsiformes
(Troutperches and relatives)

Class Actinopterygii
Order Percopsiformes
Number of families 3

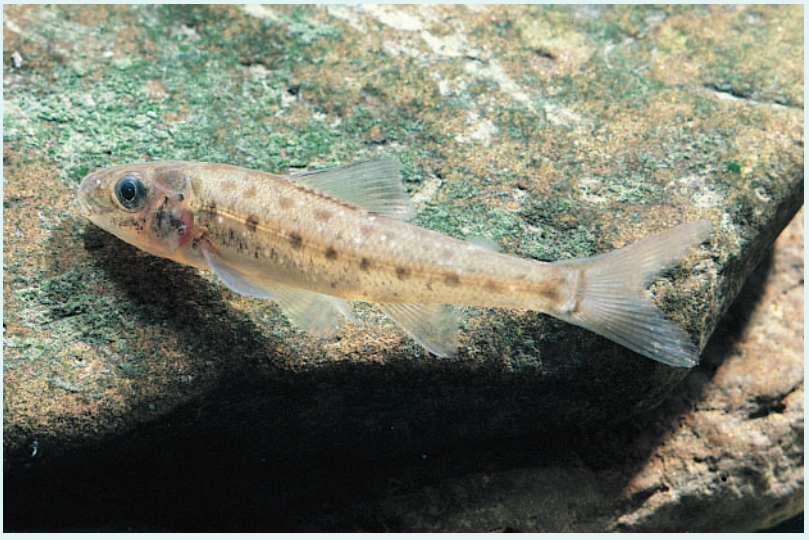


Photo: Troutperch (*Percopsis omiscomaycus*) combine the characteristics of spiny-rayed and soft-rayed fishes, resembling both trout and perch. (Photo by Animals Animals ©Raymond A. Mendez. Reproduced by permission.)

Evolution and systematics

The oldest fossils date back to the Paleocene Paskapoo Formation (between 60 and 62 million years ago) in western Canada. The Percopsiformes may be related remotely to the codfishes (Gadiformes) and toadfishes (Batrachoidiformes). One point of controversy about their phylogeny is that they show primitive conditions, such as the presence of an adipose fin, which suggests character reversal in their evolutionary history. The monophyly of this group has been questioned. Murray and Wilson proposed removal of the amblyopsid family from the group and created a new order: Amblyopsiformes.

There are two recognized suborders. The first, the Percopsoidei, is characterized by the presence of an adipose fin and a complete lateral line. The suborder is represented by one family: Percopsidae, or troutperches, with one genus and two species. The second, the Aphredoderoidei, is characterized by the absence of an adipose fin and includes two families: Aphredoderidae (pirate perch, one species) and Amblyopsidae (swampfishes and cavefishes, four genera and six species).

Physical characteristics

These are small fishes (less than 8 in, or 20 cm) with a mosaic of primitive characters, such as an adipose fin, and advanced characters, such as a pelvic girdle located farther back from the cranium compared with most other fishes. They also have fewer fin spines and ray-supported dorsal and anal fins, each usually with one to four anterior soft spines. If pelvic fins are present, they are located in a position below the abdomen and behind the pectorals, with three to eight soft rays. The body is covered with cycloid or ctenoid scales.

Distribution

The troutperches are distributed in North America from Alaska and the Great Lakes drainage to the southern and eastern United States.

Habitat

All species are freshwater, with two species found in swamps, one as a facultative cave dweller. Four species are obligatory cavernicoles (cave dwellers).

Behavior

Besides the fact that all species are solitary, little is known about their behavior. The exception is certain types of behavior studied among cavefishes. At least two of the noncavernicolous species are nocturnal.

Feeding ecology and diet

Members of this order are opportunistic predators that eat a variety of food items; at least one species is cannibalistic. Percopsiformes are preyed upon by other fishes, water snakes, and fish-eating birds. Fish larvae may be preyed upon by aquatic insects. Cavefishes are not generally preyed upon since they are the top predators in their habitats.

Reproductive biology

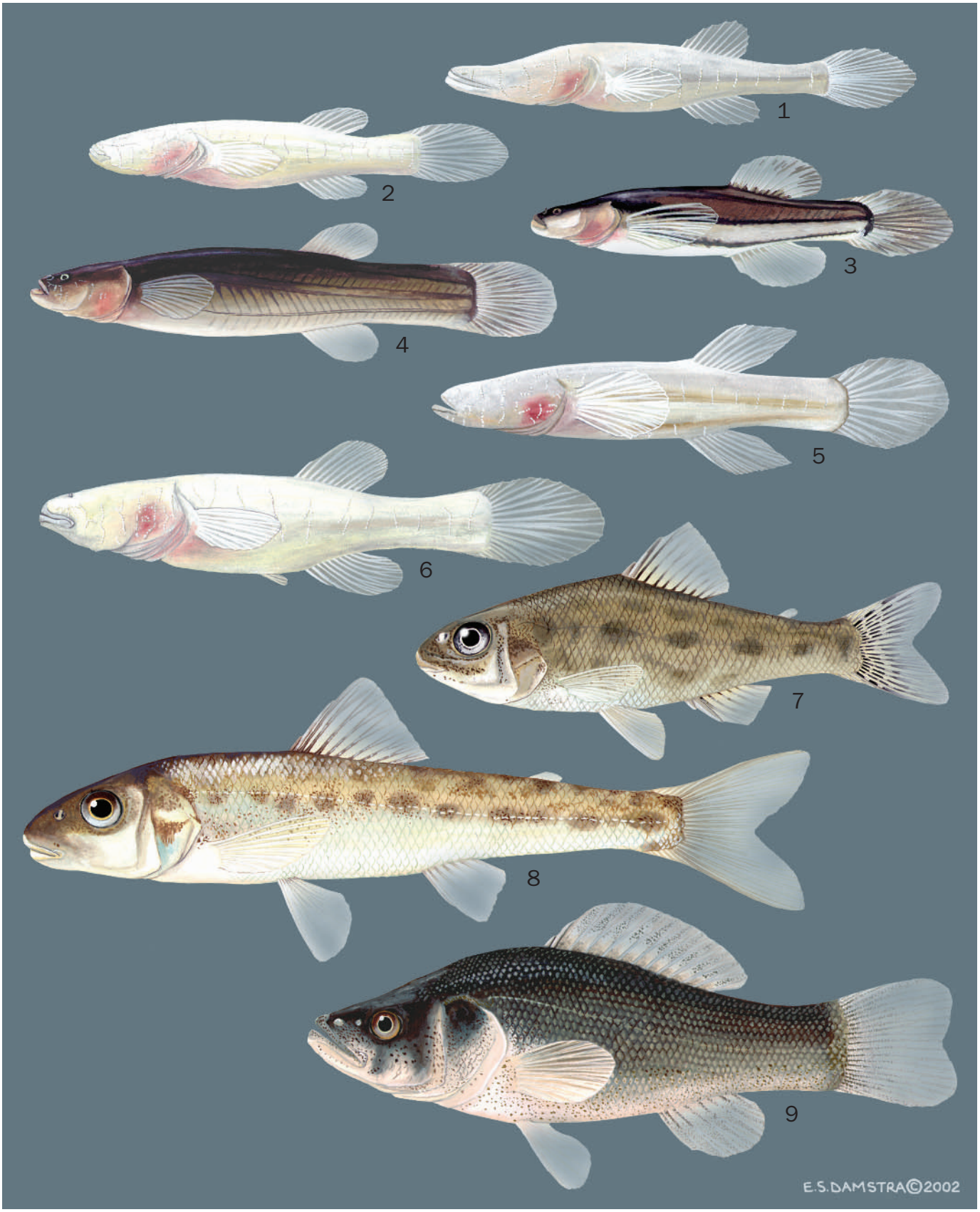
They are oviparous, but nothing else is known at the family level. Spawning (at least for the noncavernicolous species) takes place in the spring. Fecundity tends to be low.

Conservation status

The IUCN Red List includes four species from this order, all of which are cave-dwelling species from the family Amblyopsidae. *Speoplatyrhinus poulsoni* is listed as Critically Endangered, while *Amblyopsis rosae*, *A. spelaea*, and *Typhlichthys subterraneus* are listed as Vulnerable.

Significance to humans

Some species can be found in both the commercial trade and public aquaria. Cave species have been important in understanding evolutionary issues.



1. Alabama cavefish (*Speoplatyrhinus poulsoni*); 2. Ozark cavefish (*Amblyopsis rosae*); 3. Swampfish (*Chologaster cornuta*); 4. Spring cavefish (*Forbesichthys agassizii*); 5. Southern cavefish (*Typhlichthys subterraneus*); 6. Northern cavefish (*Amblyopsis spelaea*); 7. Sand roller (*Percopsis transmontana*); 8. Troutperch (*Percopsis omiscomaycus*); 9. Pirate perch (*Aphredoderus sayanus*). (Illustration by Emily Damstra)

Species accounts

Ozark cavefish
Amblyopsis rosae

FAMILY
Amblyopsidae

TAXONOMY
Typhlichthys rosae Eigenmann, 1897, "caves of Missouri."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 2.56 in (6.5 cm). Pinkish-white in coloration. The eyes are not externally visible because they have only vestigial tissue under the skin. This fish also lacks pelvic fins.

DISTRIBUTION
This species can be found at 41 sites on the Springfield Plateau, over seven counties in three states: southwest Missouri (20 sites), northwest Arkansas (10 sites), and northeast Oklahoma (11 sites). (The verified historic range was larger.)

HABITAT
Individuals of this species are found mostly in small cave streams with a chert or rubble bottom, in pools over a silt and sand bottom, or in karst windows or wells, but never too deep.

BEHAVIOR
Almost nothing is known about their behavior.

FEEDING ECOLOGY AND DIET
Stomach contents have been found to contain copepods, which constituted about 70–90% of the contents by volume; the balance was primarily small salamanders, crayfish, isopods, amphipods, and young of their own species. Most individuals grow between April and October. Cannibalism does not always occur in this species.

REPRODUCTIVE BIOLOGY
Breeding habits are not well understood. They have an extended spawning season, with a peak in late summer. The maximum life span is four to five years. Growth is sporadic.

CONSERVATION STATUS
Classified as Vulnerable by the IUCN and as Threatened by the U.S. Fish and Wildlife Service.

SIGNIFICANCE TO HUMANS
Of particular scientific interest because it is a cave species. ◆

Northern cavefish
Amblyopsis spelaea

FAMILY
Amblyopsidae

TAXONOMY
Amblyopsis spelaeus DeKay, 1842, Mammoth Cave, Kentucky, United States.

OTHER COMMON NAMES
German: Nördlicher Höhlenfisch.

PHYSICAL CHARACTERISTICS
The species grows to 4.33 in (11.0 cm). They are pink-white in coloration. The eyes are not externally visible because they have only vestigial tissue under the skin. The pelvic fins are rarely absent; when present, they are always very small. They have a large, broad head.

DISTRIBUTION
Individuals of this species are found in about 100 caves in Kentucky and southern Indiana. Based on field observations, Keith suggested that the species distribution may be limited by competition with the southern cavefish, *Typhlichthys subterraneus.*

HABITAT
Their typical habitats are caves and subterranean passages of well-developed karst terrain. Can be found on consolidated mud-rock substrates in shoals and silt-sand substrates in pools but more often in caves with uniform silt-sand substrates.

BEHAVIOR
They respond to light by moving away (scotophilia).

FEEDING ECOLOGY AND DIET
They feed on benthic crustaceans and worms but can live for two years without food because of their low metabolic rate. They are considered a top predator.

REPRODUCTIVE BIOLOGY
These fish have external fertilization, and spawning takes place during high water between February and April. They have a low reproduction rate. The females brood eggs in the gill cav-

ity for about two to five months. The young appear in late summer and early fall.

CONSERVATION STATUS
This species is classified as Vulnerable by the IUCN. It occupies a highly restricted habitat and is susceptible to any disturbance in the water, such as groundwater pollution, sedimentation, runoff, impoundment, quarrying, and overcollecting.

SIGNIFICANCE TO HUMANS
Of particular scientific value as a cave species. ◆

Swampfish
Chologaster cornuta

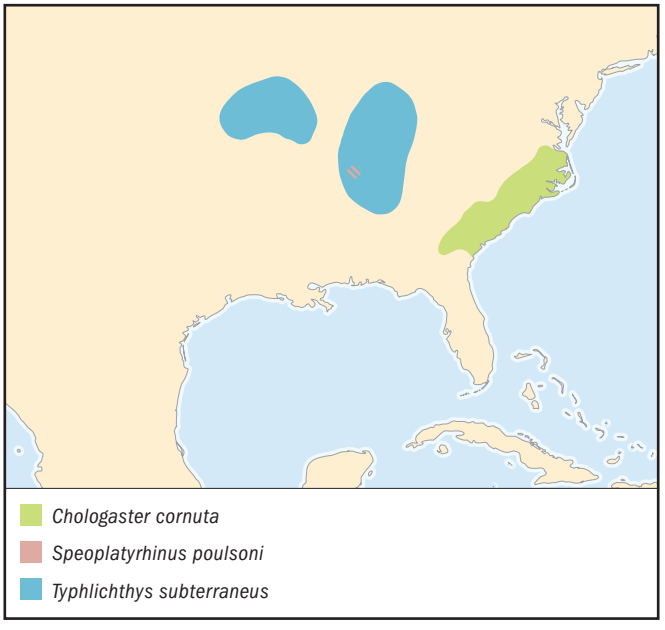
FAMILY
Amblyopsidae

TAXONOMY
Chologaster cornutus Agassiz, 1853, "ditches of the rice fields in South Carolina."

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 2.86 in (6.8 cm). These fish are strongly bicolored—dark brown above and white to yellow (creamy white) below. They also have three narrow black stripes on each side and an orange or yellow cast to the head. The head is depressed, with small eyes. Pink gills are visible through the unpigmented gill covers. The cycloid scales are embedded, and the fish lack pelvic fins.

DISTRIBUTION
This species is found in North America on the Atlantic Coastal Plain from the Roanoke River drainage in Virginia to the Altamaha River drainage in Georgia (United States).



HABITAT
They occur year-round on vegetation and debris in low-lying swamps, ponds, ditches, sloughs, and quiet pools and backwaters of streams, usually in well-shaded, small bodies of waters. The chemical nature of these waters is acidic and boglike. Often this species does not show in many faunal surveys; its sensitive response to touch (thigmotaxis) makes it difficult to find in the roots and debris of its preferred habitat along the edges of submerged weed banks.

BEHAVIOR
This species is largely nocturnal.

FEEDING ECOLOGY AND DIET
Feeds on midge larvae, ostracods, and copepods. Vulnerable to dragonfly nymphs, larger fishes, water snakes, and fish-eating birds.

REPRODUCTIVE BIOLOGY
They spawn between early March and mid-April and usually die after spawning. They lay up to 430 eggs and may live as long as two years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes found in the aquarium trade. ◆

Spring cavefish
Forbesichthys agassizii

FAMILY
Amblyopsidae

TAXONOMY
This species originally was described under two names: *Chologaster agassizii* and *Forbesella agassizi* Putnam, 1872, a well in Lebanon, Wilson County, Tennessee, United States. The genus *Forbesichthys* was eventually adopted since *Forbesella* was already in use for marine animals known as tunicates.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 3.54 in (9.0 cm). This species is dark brown to nearly black on the dorsum, grading to lighter brown laterally; it is cream yellow ventrally, often with a thin yellow stripe along each side. These fish have minute scales embedded under the skin. They lack pelvic fins and have triads of sensory papillae midlaterally and scattered clusters called neuromasts on the head.

DISTRIBUTION
Found in central and western Kentucky (west to the Tennessee River) to southern central Tennessee and west across southern Illinois to southeastern Missouri. When the Mississippi River changed its course, the Missouri population may have been isolated from the others for about 2,000 years. It was intentionally stocked from southern Illinois sites to establish a population near Quincy College. This population was intended to serve as a nearby source of fish for research.

HABITAT
Individuals of this species are active in springs at night, almost always near the surface; they usually retreat underground during the day.

BEHAVIOR
The few individuals that venture into the spring portions of their habitat may have a strong tendency to move against the current (rheotaxist) for periods of half a minute to one minute, but they typically show strong thigmotaxis and hide under rocks or debris. They prefer highly oxygenated over less oxygenated water but respond to light by moving away (scotophilia). They tolerate a wide range of temperatures.

FEEDING ECOLOGY AND DIET
They feed at night on amphipods, midge larvae, tiny worms, and microcrustaceans.

REPRODUCTIVE BIOLOGY
Spawning takes place in February. The life span is about three years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
It has no particular significance except for its ecological and scientific value in researching the process of cave colonization. ◆

Alabama cavefish
Speoplatyrhinus poulsoni

FAMILY
Amblyopsidae

TAXONOMY
Speoplatyrhinus poulsoni Cooper and Kuehne, 1974, Key Cave, Alabama, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 2.83 in (7.2 cm). This species has an extremely elongated and anteriorly depressed head that makes up one-third of the standard length in adults. The snout is laterally compressed, with a terminal mouth. The species is white in coloration and lacks externally visible eyes as well as pelvic fins.

DISTRIBUTION
Its distribution is restricted to Key Cave, Lauderdale County, on the north bank of the Tennessee River.

HABITAT
They are found mostly in still waters of cave systems.

BEHAVIOR
Nothing is known about this very rarely studied species.

FEEDING ECOLOGY AND DIET
They feed on copepods, isopods, amphipods, and other small cavefish.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of this species, and what is known is not encouraging about its future potential for survival. It appears that only a small percentage of females reproduce, producing only a few eggs, and reproduction does not take place every year.

CONSERVATION STATUS
Its total population size is estimated to be less than 100 individuals, which would make it one of the most endangered fish species in the world. It is classified as Critically Endangered by the IUCN and Endangered by the U.S. Fish and Wildlife Service. It is being threatened by groundwater pollution from agricultural runoff.

SIGNIFICANCE TO HUMANS
Of particular scientific value as a cave species. ◆

Southern cavefish
Typhlichthys subterraneus

FAMILY
Amblyopsidae

TAXONOMY
Typhlichthys subterraneus Girard, 1859, a well near Bowling Green, Warren County, Kentucky, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 3.54 in (9.0 cm). They are pinkish in coloration and have a large, broad head. The eyes are not visible, being only vestigial in nature and covered by skin. Other defining characters include seven to 10 dorsal soft rays, seven to 10 anal soft rays, 10 to 15 caudal rays, and 28 to 29 vertebrae.

DISTRIBUTION
This species is found in the subterranean waters of two major disjunct ranges separated by the Mississippi River: the Ozark Plateau of central and southeastern Missouri and northeastern Arkansas and the Cumberland and Interior Low Plateaus of northwestern Alabama, northwestern Georgia, central Tennessee and Kentucky, and southern Indiana.

HABITAT
They are found in caves near the water table.

BEHAVIOR
They do not respond to light.

FEEDING ECOLOGY AND DIET
Feeds mainly on copepods, amphipods, isopods, insects, and worms.

REPRODUCTIVE BIOLOGY
Breeding probably occurs in late spring in association with rising water levels, and spawning takes place between April and May. The females lay fewer than 50 eggs each. They grow slowly and can live up to four years.

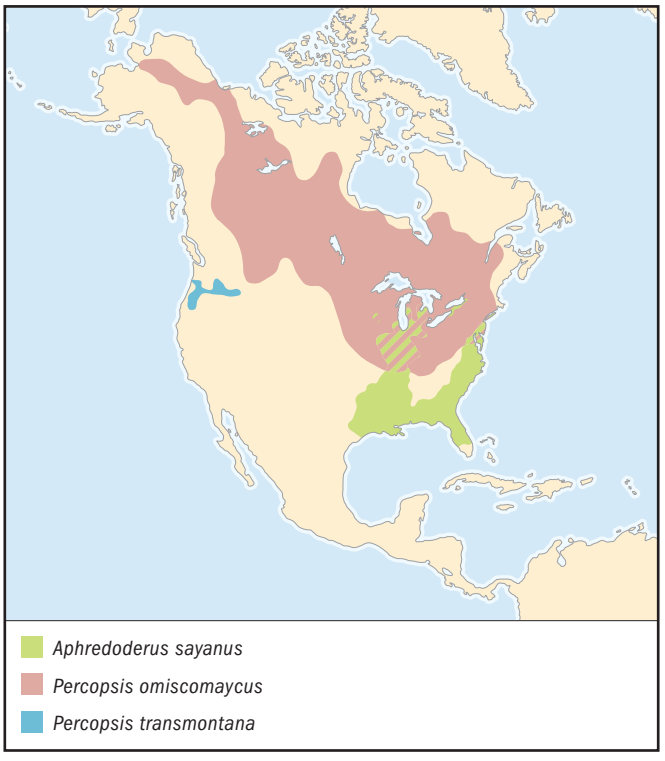
CONSERVATION STATUS
Classified as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
They are of particular scientific value as a cave species. ◆

Pirate perch
Aphredoderus sayanus

FAMILY
Aphredoderidae

TAXONOMY
Scolopsis sayanus (Gilliams, 1824), fishponds, Harrowgate, "near Philadelphia." Two subspecies have been proposed.



OTHER COMMON NAMES
German: Piratenbarsch.

PHYSICAL CHARACTERISTICS
Grows to 5.51 in (14.0 cm). A short, deep body, with a large head and mouth and a protruding jaw. They lack an adipose fin, and the lateral line is either absent or incomplete. The head is covered by ctenoid scales on the sides.

DISTRIBUTION
This species is found in waters of the Atlantic and Gulf slopes, the Mississippi Valley, and scattered parts of the eastern Great Lakes Basin in the United States from Minnesota south through the Mississippi Valley across the Gulf coast to Florida and north along the Atlantic coast to New York. It also can be found in the southeastern corner of Oklahoma, in the easternmost tributaries of the Red River, and throughout the Coastal Plain of Arkansas (but not in the Ozark Mountains). There are isolated populations in the Lake Ontario and Lake Erie drainages in New York, and the species has been reported in Wisconsin outside what is considered their native range, which suggests introduction. Populations on the Atlantic slope have been considered a subspecies (*Aphredoderus sayanus sayanus*) distinct from the subpopulation of the Mississippi Valley (*A. s. gibbosus*). The populations from the Gulf of Mexico drainage have been termed intermediate.

HABITAT
They usually occur over mud in quiet bodies of water, such as swamps, vegetated sloughs, ponds, oxbow lakes, ditches, backwaters, and pools of creeks and in small to large rivers on mud and silt bottoms. Adults most frequently are found at sites whose bottoms are overlain with leaf litter. The larvae of this species can be quite abundant in some areas.

BEHAVIOR
This is a solitary and crepuscular species.

FEEDING ECOLOGY AND DIET
They feed on insects, blue-green algae, and small crustaceans and fishes, which suggests that, like other members of this order, they are an opportunistic species that goes after almost any food item. Vulnerable to dragonfly nymphs, larger fishes, water snakes, and fish-eating birds.

REPRODUCTIVE BIOLOGY
The major spawning period for pirate perch in the Atchafalaya River Basin, Louisiana, is February through March. It appears that adult pirate perch are not branchial brooders but rather release their adhesive eggs over leaf litter and woody debris. They can live up to four years or longer.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is considered a water quality indicator species by the Arkansas Department of Environmental Quality for the Gulf Coastal Ecoregion. ◆

Troutperch
Percopsis omiscomaycus

FAMILY
Percopsidae

TAXONOMY
Salmo omiscomaycus Walbaum, 1792, Hudson Bay.

OTHER COMMON NAMES
English: Silver chub; Finnish: Lohiahven; French (Canada): Omisco.

PHYSICAL CHARACTERISTICS
Grows to 7.87 in (20 cm). Coloration can vary from yellowish to silvery to almost transparent, depending on the sexual state. There is a row of about 10 dark spots along the midline of the back and 10 or 11 spots along the lateral line, with another row of spots high on the sides and above the lateral line. The fins are always transparent. The most distinguishing characteristic is an adipose fin with small, weak spines on the dorsal and anal spines. Other characters include short gill rakers and rough ctenoid scales. The lateral line is nearly straight.

DISTRIBUTION
The original distribution was the Atlantic and Arctic basins throughout most of Canada, from Quebec to the Yukon and British Columbia, and south to the Potomac River drainage in Virginia; the Yukon River drainage, the Yukon and Alaska; and the Great Lakes and Mississippi River basins south to West Virginia, eastern Kentucky, southern Illinois, central Missouri, North Dakota, and northern Montana. It has been introduced in the Housatonic River drainage of Connecticut and Massachusetts and into Willard Bay Reservoir and Utah Lake, Utah.

HABITAT
They occur in lakes, deep-flowing pools of creeks, and rivers and usually are found over sand.

BEHAVIOR
Individuals of this species move into the shallows of lakes at night to feed and then move back to deeper water as dawn approaches. Some populations spawn exclusively at night.

FEEDING ECOLOGY AND DIET
Feeds on smaller fish, benthic crustaceans, insects, and phytoplankton. Vulnerable to larger fish, water snakes, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Spawning takes place between April and August. Two or more males compete for a single female by chasing her near the surface, often breaking the surface of the water. Eggs and milt then are released. Death has been recorded after spawning. They can live up to four years.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally used as bait. ◆

Sand roller
Percopsis transmontana

FAMILY
Percopsidae

TAXONOMY
Columbia transmontana Eigenmann and Eigenmann, 1892, near the mouth of the Umatilla River, Umatilla County, Oregon, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 3.78 in (9.6 cm). Like the troutperch, this species has a large and naked head and chambers in the lower jaws and cheeks known as "pearl organs."

DISTRIBUTION
This species is found in the Columbia River system and some tributaries from the middle Columbia River in Washington downstream to within 25 mi (40 km) above its mouth, including western Idaho, southern Washington, and northern and western Oregon, United States.

HABITAT
They occur in slow-moving portions of streams and rivers, such as backwaters and marginal pools. They prefer mud-sand bottoms, although they have been reported over rubble substrate with considerable aquatic vegetation.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Feeds on small aquatic invertebrates. Vulnerable to dragonfly nymphs, larger fishes, water snakes, and fish-eating birds.

REPRODUCTIVE BIOLOGY
Little is known, except that they can live up to six years.

CONSERVATION STATUS
Not listed by the IUCN, but the species may have disappeared from Idaho waters.

SIGNIFICANCE TO HUMANS
They have no significant economic or cultural importance to humans. ◆

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Aldemaro Romero, PhD

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Ophidiiformes
(Cusk-eels and relatives)

Class Actinopterygii
Order Ophidiiformes
Number of families 4 or 5

Photo: A pearlfish (*Carapus bermudensis*) about to enter a sea cucumber. (Photo by Chesher/ Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Ophidiiformes is a group of slender, elongate, eel-like, and mostly bottom-dwelling fishes that is relatively unremarkable in external morphological features but exhibits highly evolved behavioral and reproductive traits. The order contains 355 named species, but there are numerous undescribed forms in scientific collections that have not been formally named. Collectively, there are probably 380–400 ophidiiform species in 90 genera, living mostly in marine environments but also including some freshwater and estuarine species. The order has the deepest-dwelling fish known to science, *Abyssobrotula galatheae*, captured at a depth of approximately 5 mi (8,370 m) below the ocean surface! The ophidiiform family Carapidae (the pearlfishes) comprises about 31 species in seven genera, including some species that are parasitic in the body cavities of marine invertebrates, such as starfish and sea cucumbers. The family Ophidiidae, the cusk-eels, is the most diverse family (about 218 species in 48 genera) and includes several large benthic species that are fished commercially. The family Bythitidae contains 96 species in 32 genera and includes live-bearing species that reside in shallow waters. The family Aphyonidae contains 22 live-bearing species (in six genera) that occur in deeper waters. Another family, the Parabrotulidae (three species in two genera), often is included in the order Ophidiiformes, but its placement there is the subject of controversy. Some researchers consider parabrotulids to be close relatives of the perciform family Zoarcidae, the eelpouts. Parabrotulids, however, share with Ophidiiformes many skeletal and soft anatomical features that are lacking in zoarcids. Thus, the taxonomic limits of the order Ophidiiformes remain uncertain and require further research.

The cusk-eels and their allies are classified in the superorder Paracanthopterygii, a large and morphologically diverse assemblage that includes the freshwater trout-perch and its relatives (Percopsiformes), the codfish and its relatives (Gadiformes), and the goosefish and its relatives (Lophiiformes). Some ichthyologists doubt that the Paracanthopterygii is a natural grouping (that is, monophyletic, or derived from a common ancestor), and the superorder has been reorganized several times. At present the superorder is defined by the common possession by its members of certain skeletal traits of the caudal fin and the cranium as well as the presence of a small bone (termed a supraneural) that lies in the dorsal musculature above the anterior vertebrae. Some paracanthopterygian fishes also possess certain morphological traits that are characteristic of the higher perchlike fishes (Acanthomorpha). These traits include the presence of true fin spines, particular patterns of small bones and ligaments associated with anterior vertebrae, and patterns of ossification of the pelvic bones. Thus, it is generally accepted that the Paracanthopterygii are acanthomorph fishes, currently classified within the Holacanthopterygii, a newly proposed name for a higher category that includes stephanoberyciform, zeiform, beryciform, and all other perchlike fishes. Within the Paracanthopterygii, ophidiiform fishes may be aligned most closely with gadiformes. Ophidiiforms and gadiforms share certain structural and developmental features of the caudal skeleton and gut anatomy. The phylogenetic relationships among paracanthopterygian orders remain speculative, however.

Extensive morphological analysis has not produced a satisfactory hypothesis of the evolutionary history of the ophidiiform fishes, and the phyletic relationships among ophidiiform families are largely unknown. Within the order, ichthyologists have shown natural groupings at family, subfamily, and generic levels, and there are solid proposals for sister group relationships among some families. Evidence for monophyly of the entire ophidiiform lineage is lacking, however. A number of

characters have been proposed to classify ophidiiform families, including the position of the pelvic fins, but most of these proposals have proved unsatisfactory. Ichthyologists currently subdivide ophidiiform fishes into two groups, based on the presence or absence of viviparity and the anatomical features that are associated with live bearing.

The suborder Bythitoidei (containing the live-bearing families Bythitidae and Aphyonidae) is considered to be a natural grouping, since it is apparent that these fishes share highly specialized reproductive traits. Within the suborder, aphyonids and bythitids are sister taxa, each possessing uniquely specialized morphological characters (termed "synapomorphies"). Ichthyologists have been unable to specify synapomorphies supporting monophyly of the suborder Ophidioidei (containing the oviparous Carapidae and Ophidiidae), however. Within the Ophidioidei, the Carapidae has been shown to be monophyletic and is considered the closest relative of all other ophidiiforms. The Ophidiidae has not been shown to be monophyletic, but there are natural groupings within the family. The ophidioid subfamily Ophidiinae (the true cusk-eels) is considered monophyletic, because all its members share certain characteristics of the pelvic girdle. The ophidioid subfamilies Brotulinae and Brotulotaeniinae each contain a single, well-defined genus. The ophidioid subfamily Neobythitinae, containing 38 genera and about 170 species, is probably not a natural group and requires further research.

Fossil evidence of paracanthopterygian fishes is not extensive. A freshwater Paleocene fossil taxon, *Mcconichthys*, may be associated with the ophidiiform lineage, but this conclusion is disputed by some researchers. Fossil ophidiiform fishes, especially fossilized otoliths, or ear bones, are abundant in some Tertiary deposits. To date, several ophidiiform taxa have been described from the Paleocene and Eocene and from more recent deposits, including species of *Hoplobrotula* and *Ampheristus*.

Physical characteristics

Most ophidiiforms are long, relatively slender fishes with big heads, often small eyes, long dorsal and anal fins, and a caudal portion that tapers to a point. Sizes range from the tiny *Microbrotula*, which matures at 1.5 in (38 mm) in length, to commercially exploited species such as *Genypterus blacodes* that attain lengths of 3.3–6.6 ft (1–2 m). The cusk-eels often are strongly pigmented along the dorsal or anal midline, with lateral black or brown markings or bands extending the length of the body. In other ophidiiforms, the body is covered uniformly with small pigment spots, or pigment is entirely lacking. The mouth usually is large, and the upper jaw (maxilla) reaches a point at or beyond a vertical drawn through the eye.

A cusk-eel (*Ophidion scrippsae*) swimming near southern California. (Photo by Kerstitch. Bruce Coleman, Inc. Reproduced by permission.)

The caudal fin is small, sometimes reduced to a bony point, never forked, and often inconspicuous when it is confluent with the dorsal and anal fins. The pectoral fins often are long, sometimes exceeding the length of the head. The pelvic rays sometimes are absent. When present, the pelvic rays usually are long and conspicuous. Scales can be absent, but when present, they generally are small. The order is defined by the following set of external characteristics. (1) The pelvic fins (when present) have only one or two rays. (Some species have an additional spinelike splint.) (2) The pelvic fins are inserted anteriorly, just below the opercular margin or sometimes farther forward. (3) The pelvic fin bases typically are close together. (4) The dorsal and anal fin bases are long, reaching the caudal fins in most species. (5) There are no dorsal or anal fin spines. (6) Bones (termed "pterygiophores") supporting the anal- and dorsal-fin rays outnumber total vertebrae. (The ratio of dorsal and anal rays to total vertebrae is about 1.5:1.) (7) The nostrils are paired on each side of the head.

In the pearlfishes (Carapidae), the anal-fin rays are longer than the dorsal-fin rays, and the upper jaw lacks a supramaxillary bone. In ophidiids the supramaxillary bone is present, and the anal-fin rays are either equal in length or shorter than the dorsal-fin rays. Within these families, subfamilies are distinguished on the basis of the presence or absence of pelvic fins, scales, barbels, and other internal traits. Carapids and ophidiids are egg-laying fishes, and males lack the external intromittent organ that is characteristic of bythytoid fishes. In addition, the nostrils of ophidioid fishes are positioned higher on the snout than those of bythytoid fishes. Bythytids possess a swim bladder, and most species have scales; aphyonids lack both scales and a swim bladder. Bythitid subfamilies are distinguished by caudal-fin morphological features. Aphyonids are fragile, transparent fishes that have weakly developed skeletal systems and possess other traits characteristic of larval ophidiiforms. Thus, many ichthyologists believe that aphyonids are neotenic. Neotenic organisms are those that retain larval features as adults, and the process of neoteny is thought to be important in the evolution of many animal species, including humans.

Distribution

Most ophidiiform fishes are distributed broadly in all oceans, sometimes to abyssal depths and extending to shallow seas and estuaries. Ophiidiforms occur from Greenland south to the Weddell Sea, but most species are found in warmer waters of the tropics and subtropics. Carapids, ophidiids, and aphyonids are strictly marine, whereas some bythitid species are estuarine or reside in freshwater. Some bythitids have extremely restricted home ranges in caves and sinkholes.

A pearlfish (*Carapus bermudensis*) living inside a sea cucumber. (Illustration by Patricia Ferrer)

Habitat

Ophidiiform fishes generally are secretive and tend to associate with structures or with other animals. Most opidiiforms are free-living benthic species hovering close to the bottom and residing in mucus-lined mud or sand burrows, rock or coral crevices, or sea caves or associated with bottom-dwelling invertebrate communities, including deep sea vent fauna. Some species are pelagic or benthopelagic. One mesopelagic genus is associated uniquely with a species of deep-sea jellyfish. Pearlfishes are either free-living or inquiline species. Free-living species (the pyramondontimes and some echiodontines) are pelagic or bottom dwelling in deep oceanic water or on the continental shelf. Some echiodontines are believed to be associated with tube worm communities. The commensal carapids (*Onuxodon*, *Carapus*, and *Encheliophis*) are all shallow-dwelling species that reside within the body cavity of invertebrate hosts, such as pearl oysters, giant clams, tunicates, sea stars, and sea cucumbers. Species in the bythitid genera *Lucifugia* and *Ogilbia* reside in freshwater caves and sinkholes.

Behavior

The air bladder, anterior vertebrae, and associated ligaments and muscles are modified in many ophidiiform fishes to produce sound. In some species, the air bladder is partly ossified and serves as a resonating chamber. Sound production is thought to be associated with reproduction, as some species have been observed to produce sound just before mating. Hydroacoustic surveys often show large assemblages of vocal cusk-eels. Ophidiiform fishes generally have a close association with the bottom, hovering near holes, ledges, and drop-offs or hiding in mud and sand. Burrowing is accomplished by tail-first entry into soft and movable sediments. Ophidiiform fishes usually hide in burrows or crevices or within or around invertebrate hosts during daylight hours and then exit at night to forage. One bythitidae species has been seen living inside a hot thermal vent at great depths. Many ophidiiform fishes have highly evolved commensal associations with invertebrates. In the pearlfishes, some species are obligatory inquilines that never leave their hosts and feed on a host's internal organs.

Feeding ecology and diet

Ophidiiform fishes consume a wide variety of invertebrate and fish prey. Most are bottom dwellers that are strongly nocturnal, suggesting that they forage for benthic organisms during evening hours. This feeding behavior is facilitated by well-developed sensory pores on the head; a large, inferior mouth; and long, fleshy barbels on the chin in some species that are believed to aid in locating prey. Food consists of worms, crustaceans, echinoderms, and small bottom fishes such as gobies and small flatfishes. In turn, ophidiiform fishes are important food sources for many larger fish predators including skates, rays, sharks, eels, cod, hakes, goosefishes, and flounders. In addition, cusk-eels and their relatives living in shallow waters are prey to wading birds.

Reproductive biology

Ophidiiform fishes either deposit eggs or bear live young. The oviparous (egg-bearing) species include the pearlfishes (Carapidae) and the cusk-eels (Ophidiidae). Eggs of most carapids and ophidiids are unknown. Those that have been identified either are spawned in open water as individual, free-floating eggs or are deposited in a mucilaginous raft or gummy matrix, much like eggs of the goosefish and its allies (Lophiiformes). The egg rafts float at the ocean surface until they hatch, usually within several days. Larvae of carapids and ophidiids are pelagic, typically floating near the surface and sometimes traveling great distances from their hatching locality. Scientists believe that larvae of these species have the ability to regulate growth and metamorphosis (the transformation to juvenile and adult form). This developmental strategy allows species to disperse over great distances into habitats that are underutilized, thus reducing competition for limited resources.

Pearlfish larvae are unique in their possession of a long, highly ornamented predorsal filament (actually, the first dorsal fin ray), known as the vexillum. The vexillum may have a sensory function, because it contains stout cranial nerve fibers and its position around the head and mouth can be controlled by the larva. Vexillifer larvae have been identified for almost all pearlfish genera. Larvae are elongate, and their bodies typically are sparsely pigmented. After a long pelagic period, vexillifer larvae of species that are commensal or parasitic in invertebrates as adults lose the vexillum and shrink in length to transform abruptly to a so-called tenuis stage. The tenuis larvae seek out their benthic invertebrate hosts before maturing into adults.

Most cusk-eel larvae do not undergo an abrupt transition in morphological features in their development. One remarkable exception is a strange larva captured near South Africa. The larva has an enormous appendage that is highly pigmented and resembles the tentacles of a jellyfish. The appendage contains the larval gut. This so-called exterilium larva ("the larva with an outside gut") is tentatively identified as an unknown ophidiid species. Larvae of the ophidiid subfamily Neobythitinae have elongate dorsal and pelvic rays, but all other larval cusk-eels lack elongate rays. These larvae generally resemble adults, with a conspicuous coiled gut, pelvic fins placed far forward on the throat, long dorsal and anal rays, and big heads and mouths.

Larvae of the live-bearing bythytoid fishes are poorly known, and only a few have been described. Larvae of *Brosmophysis* (Bythitidae) and *Barathronus* (Aphyonidae) generally resemble ophidiid larvae, in that they lack elongate rays and possess coiled guts and long dorsal and anal fin bases. Aphyonid larvae hatch at larger sizes than do bythitid larvae. Some bythytoid embryos have specialized feeding appendages termed "trophotaena," through which they gain maternal nourishment. Some bythytid embryos consume or suckle bulbs of ovigerous tissue during development to supplement embryonic nutrition through the yolk sac.

Conservation status

The IUCN lists seven ophidiiform species as Vulnerable due to their rarity and limited habitats. All are live-bearing bythytids: *Lucifugia* (*Stygicola*) *dentata*, *L. simile*, *L. spelaeotes*, *L. subterranea*, *L. teresianarum*, *Ogilbia pearsei*, and *Saccogaster melanomycter*. One species, *O. galapagosensis*, is listed as Data Deficient.

Significance to humans

Most ophidiiform fishes are unknown to the public and are rare, deep-water species taken only in research cruises or commensal and parasitic forms that hide inside the bodies of invertebrate hosts or otherwise secretive species living in caves or small crevices in the reef. Four species in the genus *Genypterus* are large; their flesh is tasty, and they are fished commercially. In Chile and New Zealand, landings of *G. blacodes* reach 33,000 tons (30,000 metric tonnes) annually. *Brotula barbata* is a food source of growing importance to the peoples of several west African countries.

1. Key brotula (*Ogilbia cayorum*); 2. Pearlfish (*Carapus bermudensis*); 3. Band cusk-eel (*Ophidion holbrooki*). (Illustration by Patricia Ferrer)

Species accounts

Key brotula
Ogilbia cayorum

FAMILY
Bythytidae

TAXONOMY
Ogilbia cayorum Evermann and Kendall, 1898, Key West, Florida, United States. The holotype is a female. It was unknown at the time of the original description that the species is sexually dimorphic. Thus, considerable taxonomic confusion occurred when the male of the species was described separately. Taxonomic confusion persists, since it is believed currently that numerous undescribed *Ogilbia* species reside in the western tropical Atlantic Ocean. The extent to which their distributions overlap with the Key brotula is unknown. Thus, care must be taken in identification.

OTHER COMMON NAMES
English: West Indies brotula.

PHYSICAL CHARACTERISTICS
A small and moderately elongate ophidiiform fish with long anal and dorsal fins. The body and fins are uniformly pigmented, appearing yellow to olive-brown. Adults can attain about 3.9 in (10 cm) in length. The caudal fin is distinct and separate, not confluent with the dorsal- and anal-fin bases. The pelvic fins are positioned at the isthmus, anterior to the pectoral-fin bases. Each pelvic fin has one fleshy ray that is longer than the length of the head. The eye is small and the mouth large, with the upper jaw extending well posterior to the eye. The body is covered with small overlapping scales that do not appear on the cheeks (opercular bones).

DISTRIBUTION
The species is known from the Florida Keys, the Bahamas, and other localities in the Caribbean, including Belize, Cuba, Puerto Rico, and Jamaica south to Venezuela. Many of these distributional records may be for undescribed and similar species with overlapping distributions in this region.

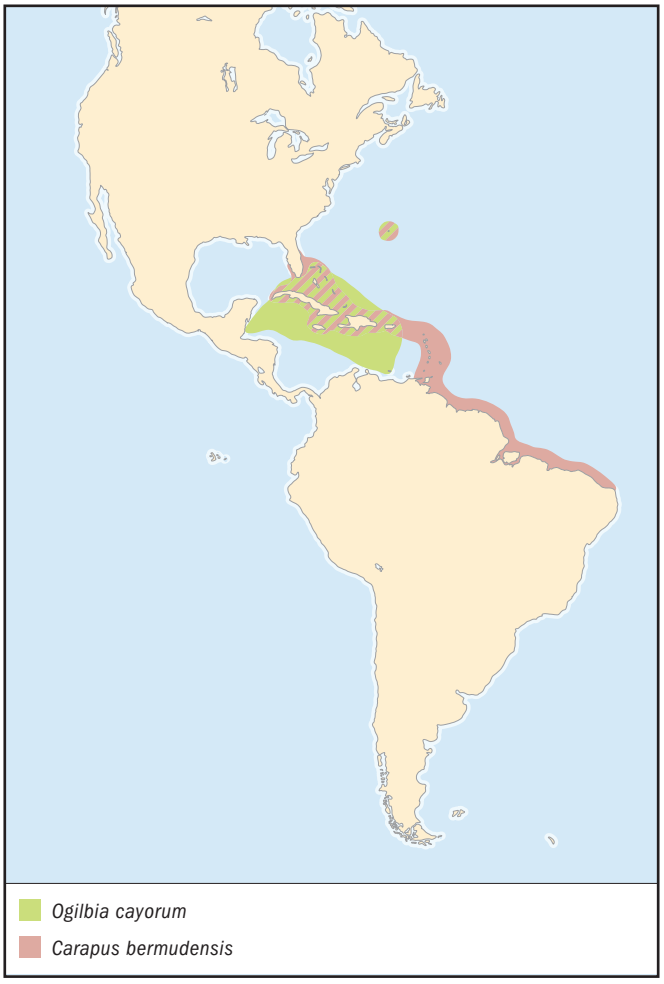
HABITAT
The holotype of the Key brotula was collected by seine on an algae-covered shoal over coral rubble. The coral fragments were encrusted with organisms. The species usually is collected at depths of less than 9.8 ft (3 m), often by uprooting and shaking clumps of *Halimeda.* This secretive bythitid also may reside in reef crevices, rocky holes, and mangrove roots in shallow waters and out to the edge of the reef. It is rarely seen by divers and typically is collected only in research surveys at poison stations, sometimes locally abundant. For example, more than 15 individuals were collected at one station in Belize. The species probably is tolerant of large fluctuations in temperature and salinity.

BEHAVIOR
Specimens kept in aquaria constantly hide under shells or rubble. The species probably is nocturnal, judging by its small eyes and cryptic nature. There are few data on its natural habits.

FEEDING ECOLOGY AND DIET
There are no detailed studies of the diet or feeding behavior of this species. Juvenile and adult Key brotulas probably eat small crustaceans and are preyed upon by larger fishes and wading birds. Embryonic nutrition is remarkable. To supplement energy reserves in yolk sacs, embryos of Key brotula "suckle" on fluid-filled bulbs of ovigerous tissue. This highly unusual developmental strategy may be an evolutionary response to the poor feeding evironment of larvae after hatching.

REPRODUCTIVE BIOLOGY
Males and females have delicate, interlocking copulatory organs. Genital morphological features have been described in detail, but mating has never been observed. The copulatory apparatus of the male is partly calcified and is thought to be derived from the first anal ray. The penis rests on a pedestal surrounded by muscular pseudoclaspers and covered by a fleshy urogenital hood. The urogenital pore of the female is similarly protected. Most bythitids have the capability of sperm storage in the oviduct or ovary. Fertilization is internal, and embryos grow rapidly. Late embryos are well developed, with pigmented eyes and fully developed and functional digestive system, musculature, gills, and caudal fin. Newborn young are about 0.5 in (12 mm) in length, and brood size is about 14 individuals.

CONSERVATION STATUS
Not listed by the IUCN.



SIGNIFICANCE TO HUMANS
This species is rarely observed and is not fished commercially. It has limited appeal as an aquarium species, since it rarely shows itself to the viewer. ◆

Pearlfish
Carapus bermudensis

FAMILY
Carapidae

TAXONOMY
Lefroyia bermundensis Jones, 1874, Bermuda. The holotype was named in honor of Lefroy, a former governor of Bermuda. The species is now valid as *Carapus bermudensis* (Jones) following several taxonomic revisions. Numerous names are probably referable to *C. bermudensis*, including *C. recifensis*, *C. chavesi*, and *Fierasfer dubius. C. bermudensis* may be related most closely to *C. acus*, its eastern Atlantic relative. The species-level relationships of the genus, however, are poorly known.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Carapus bermudensis is long, slender, and eel-like, with a large head and relatively large eyes. It is translucent, with silvery bands along the flanks, black internal pigment visible along the vertebral column, a silver cheek patch, and large pigment blotches along the bases of the dorsal and anal fins and head. The anal fin origin is anterior to the dorsal fin origin. There are 13–18 anal rays anterior to the first dorsal ray. This number varies among pearlfish species and is useful in identification. There are no pelvic fins, and the caudal fin usually is absent. The pectoral fin has 17–20 rays. The teeth on the upper jaw are small, and some are heart-shaped. The teeth on the lower jaw are larger and conical. The air bladder is separated into two parts by an internal constriction under vertebrae 11 and 12. This feature of the internal anatomy is characteristic of all species in the genus *Carapus*, and the position of the constriction relative to the vertebrae allows for separation of species.

DISTRIBUTION
Distributed in shallow waters along the shores of the western Atlantic, Bermuda, and the Caribbean Sea south to Brazil. Its larvae sometimes are collected far north and east of this range in plankton samples taken by research cruises.

HABITAT
All species of the genus *Carapus* have obligatory commensal relationships with sea cucumbers (Holothuria), starfishes (Asteroidea), or sea squirts (Ascidiacea). Many species exhibit host specificity. *Carapus bermudensis* has been collected in the body cavity of nine holothurian species in the genera *Actinopyga*, *Isostichopus*, *Thone*, *Astichopus*, *Holothuria*, and *Theelothuria.* These host species generally reside in shallow waters, to about 98.4 ft (30 m) on sandy bottoms or grass beds in tropical and subtropical lagoons near reefs. In one study in the Bahamas, pearlfishes were found in relatively few restricted areas, although more than 1,000 sea cucumbers were surveyed.

BEHAVIOR
Resides within the body of its host during daylight and is believed to exit at night to forage and perhaps spawn. This strategy limits the probability of predation by larger fishes. This species has been observed in aquaria as it rapidly enters its primary host, *Actinopyga agassizi.* The species first locates the anal opening of the sea cucumber with its snout, presumably through olfaction. As the fish holds its head in the proper position at the anal opening, the body curves and the tip of the tail tracks along the mid-lateral line until it reaches the anus. Once the tail tip is aligned and pointed into the opening, the fish abruptly turns, forcing its way tail first into the host by body undulations. There are no observations of living pearlfishes in the wild and little data on its habits and behaviors.

FEEDING ECOLOGY AND DIET
Some inquiline pearlfishes are parasitic, dining on the internal organs of the invertebrates they occupy. This species of pearlfish is not parasitic and feeds outside the holothurian host, probably at night. There have been no detailed studies of the food habits of this species, but gut contents of individuals are mostly crustacean invertebrates, such as amphipods, small shrimps, crabs, and mysids. Rarely, a pearlfish is found in the stomach of larger, predaceous fishes.

REPRODUCTIVE BIOLOGY
Spawning of pearlfishes has not been observed, and carapid reproductive behavior is poorly known. Some investigators have identified eggs collected in plankton samples by subsequent incubation in the laboratory. There also are a few reports of pearlfish species spawning in aquaria. In these cases, the scientists did not observe spawning directly but found eggs in tanks after periods of darkness. The eggs of pearlfishes are ellipsoid, usually containing an oil droplet and deposited into a jellylike, mucous matrix that floats at the surface. The egg mass has been described as oval, spherical, or somewhat flattened. Eggs hatch in one to two days. Early larvae are easily identified, since they possess a vexillum that first appears as a small protuberance but rapidly grows in length. Older pearlfish larvae have a long pigmented and ornamented vexillum that often is damaged in collection. Pearlfish larvae are extremely elongate, reaching about 7.1 in (180 mm) in length, and possess a distinct small ring of melanophores on the snout. Larvae are remarkable, in that they undergo two separate growth phases: the first as vexillifer larvae that become very elongate and the second as tenuis larvae that shrink to about half their original length.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is rarely observed and is not fished commercially. ◆

Band cusk-eel
Ophidion holbrooki

FAMILY
Ophidiidae

TAXONOMY
Ophidium holbrooki Putnam, 1874, Key West, Florida, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Variations in squamation (scale pattern), counts of fin rays, vertebrae, and other skeletal features, and body coloration are

often useful in identifying ophidiid fishes. The band cusk-eel lacks scales on the top of the head and has 66–69 total vertebrae, 117–132 dorsal rays, 977–109 anal rays, and 19–21 pectoral rays. The dorsal and anal fins are continuous with the caudal fins. The pelvic fins, each consisting of two rays, are located far forward on the chin. The head and the body are tan in color, with no mottled patterns, blotches, or bands of pigment. The dorsal and anal fins are edged in black. This species is larger, attaining about 11.8 in (30 cm) in total length, and somewhat deeper bodied than other cusk-eels (genera *Ophidion*, *Lepophidium*, *Otophidion*, and *Parophidion*) found in its home range.

DISTRIBUTION
Along the Atlantic coast of the United States from North Carolina south to the Gulf of Mexico and extending along the coast of Brazil to Lagoa dos Patos. The species is reported to be absent from the Bahamas.

HABITAT
Little is known of the specific habitats of the band cusk-eel. It has been collected with research and commercial trawls on soft muddy to sandy bottoms from near shore to about 246 ft (75 m).

BEHAVIOR
There have been no studies of the behavior of this species. Ophidiid fishes are bottom dwellers, and many reside in burrows dug into soft mud and sand. Observations by sumersibles suggest that some ophidiid species are nocturnal and abundant in some areas. Many, perhaps all, cusk-eels produce sound, and recent acoustic surveys have found large and vocal assemblages of ophidiid fishes in some areas. Sound production most likely is related to spawning behavior.

FEEDING ECOLOGY AND DIET
There have been no studies of the feeding habits of the band cusk-eel. Ophidiid fishes consume benthic invertebrates, primarily small crustaceans (shrimps, amphipods, mysids, and crabs) and worms. Small fishes, such as anchovies, gobies, and tonguefish, also are consumed. In turn, the band cusk-eel is preyed upon by larger fishes, especially dogfish, skates, conger eels, and flounders.

REPRODUCTIVE BIOLOGY
Unlike bythytids, male band cusk-eels do not have a copulatory organ, and fertilization occurs externally. The eggs and larvae have not been described, and the early life stages of this and most cusk-eel species are unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is landed as by-catch in trawl fisheries for shrimps and bottom fishes and may appear in fish markets in some countries of South America. It is relatively small and has limited value in commercial markets, although its flesh is considered good. ◆

Resources

Books

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Robins, C. Richard, and Carleton R. Ray. *A Field Guide to Atlantic Coast Fishes of North America.* Boston: Houghton Mifflin Co., 1999.

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Johnson, G. D., and C. Patterson. "Percomorph Phylogeny: A Survey of Acanthomorphs and a New Proposal." *Bulletin of Marine Science* 52 (1993): 554–626.

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John E. Olney, PhD

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Gadiformes

(Grenadiers, hakes, cods, and relatives)

Class Actinopterygii
Order Gadiformes
Number of families 11

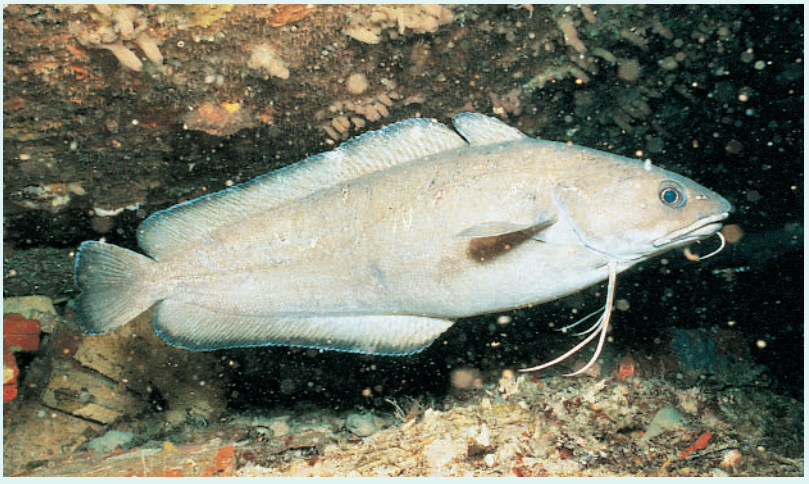


Photo: A hake, or forkbeard (*Urophycis blennoides*), in the Mediterranean Sea. (Photo by Sophie de Wilde/Jacana/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

It is important to note that agreement is lacking among ichthyologists as to the composition, origins, hierarchy, or relationships within the Gadiformes. Nor is there agreement concerning external relationships of members of this rather arbitrary group of fishes. There are no groupings of characteristics that can be assigned to the Gadiformes alone; therefore, synapomorphies (derived characters shared by all members of the group in question) have not been identified for all members of the order to the exclusion of nonmembers. Important recent contributions concerning the phylogeny and systematics of the order Gadiformes include Marshall and Cohen 1973; Markle 1982; Cohen 1984; Fahay and Markle 1984; Cohen (Ed.) 1989 (and several contributions therein); and Cohen et al. 1990. To quote Cohen et al. "The assignment to the order of many species is presently as much a matter of ichthyological convention as it is a result of logic." For the purposes of the present volume, we ground our classification on a taxonomic model proposed by Cohen et al. 1990, wherein taxa are listed alphabetically, in order not to suggest phylogenetic relationships. However, we elevate several genera or groups of genera to family status, not arbitrarily, but based on a consensus of several studies. Those 11 families are listed below (alphabetically) with a tally of genera and species presently understood to be contained in each.

- Bregmacerotidae (1 genus, 15 species)
- Euclichthyidae (1 genus, 1 species)
- Gadidae (12 genera, 22 species)
- Lotidae (3 genera, 4 species)
- Macrouridae (19 genera, 300+ species)
- Melanonidae (1 genus, 2 species)
- Merlucciidae (3 genera, 18 species)
- Moridae (18 genera, 89 species)
- Muraenolepididae (1 genus, 4 species)
- Phycidae (6 genera, 27 species)
- Steindachneriidae (1 genus, 1 species)

This listing departs from certain other studies presently available in the following ways: 1) The Gadidae, Lotidae, and Phycidae are usually considered subfamilies (Gadinae, Lotinae, and Phycinae) of the family Gadidae in those studies; 2) the genus *Steindachneria* is included in the Merlucciidae in some other studies rather than being elevated to full family status; and, 3) the Merlucciidae is included in an expanded family Gadidae in some other studies. The listing above is used here largely because it is the result when ontogenetic evidence is considered. It also better emphasizes the diversity present within the order Gadiformes.

Physical characteristics

The families listed above are diagnosed as follows:

- Bregmacerotidae: These species are sometimes called unicorn cods. The first dorsal fin is a single, elongate ray arising from a position over the head. The second dorsal and anal fins are long mirrors of each other; there are longer rays at the anterior and posterior ends forming rounded lobes. The elongate, trailing pelvic fin rays arise from the throat position and extend well beyond the anus. The lateral line is high on the body and is parallel to the dorsal margin of the body. There are no chin barbels.
- Euclichthyidae: The single species is called the eucla cod. The body is long and tapering to a very narrow caudal peduncle. It has a large mouth and no chin barbel. The first dorsal fin is short and high,

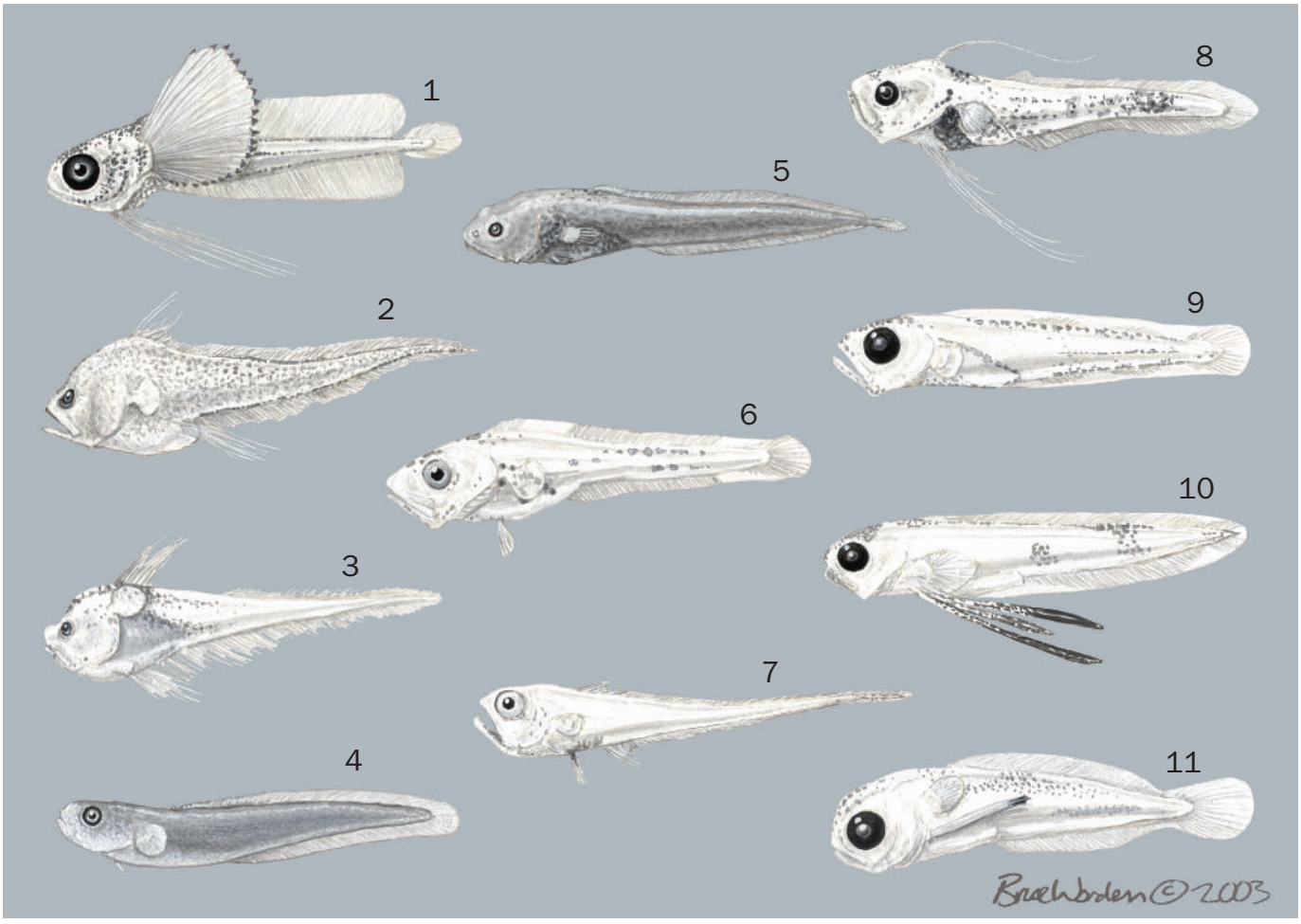
nearly touching the second dorsal fin, which is shorter and extends the length of the body to the caudal fin. The anal fin is long, with a greatly enlarged anterior lobe. The caudal fin is small and asymmetrical, with the lower rays being longest. Each pelvic fin is comprised of four separate, filamentous rays.

- Gadidae: This family includes cods, haddock, pollock, tomcod, and others. There are three separate dorsal fins and two separate anal fins. The dorsal and anal fins are either touching at their bases or separated by gaps. A chin barbel is usually present. There are pelvic fins, sometimes with one or more elongate rays.
- Lotidae: This includes the tusk (or cusk), burbot, and lings. The dorsal fin is single (in *Brosme*), or there is a short first dorsal followed by a long second dorsal in *Lota* and *Molva*. The single anal fin has a long base and includes many fin-rays. There is a well-developed chin barbel. The pelvic fins are normal and are not modified into elongate rays.
- Macrouridae: This includes rattails and grenadiers. The head and trunk are short, and the tail is compressed and greatly elongate, tapering to a point and lacking a caudal fin (with one exception). The chin barbel is usually present. The head and mouth shape and size vary. Eye size varies, but eyes are usually very large. There are two dorsal fins; the first is high, often including spinous anterior rays. The second dorsal and anal fins are long, meeting at the tail tip. The pectoral fins are narrow based and positioned high on the trunk. The pelvic fins are narrow based, thoracic to jugular in position, and comprised of 5–17 rays. Some species have a light organ on the mid-ventral line of the trunk. The benthic species have a well-developed air bladder, and the bathypelagic species lack an air bladder.
- Melanonidae: This includes the pelagic cod. It is small, not exceeding 5.9 in (15 cm). The body is long, tapering to a very narrow caudal peduncle. The head has numerous fleshy ridges. There is no chin barbel. The dorsal and anal fins are single and long-based. A slight gap separates the caudal fin from the dorsal and anal fins.
- Merlucciidae: This includes hakes and grenadiers. The genus *Merluccius* (hakes) has a large head (1/3 to 1/4 of body length), with a large, oblique mouth. The lower jaw is longer than the upper. There are two separate dorsal fins, with the first being short-based, high, and triangular. The second is long and partially divided by a notch in midsection. The single anal fin is similar in shape to the second dorsal. There are pelvic fins with seven rays. The genera *Lyconus* and *Macruronus* are characterized by long, tapering bodies lacking caudal fins. The dorsal fin is single with elevated anterior portion in the former, double with short first dorsal followed by very long second dorsal in the latter. Both have large, oblique mouths. Both have normal pelvic fin without elongate rays. The pectoral fin includes elongate rays in *Lyconus*.
- Moridae: This includes the moras. The body tapers to a very narrow peduncle. There are two or three dorsal fins, and one or two anal fins. The pelvic fins are thoracic and are wide apart at the bases. The caudal fin is symmetrical and separated from the dorsal and anal fins by a gap.
- Muraenolepididae: This includes moray cods. The body is long and compressed. The head is small with a chin barbel. The gill openings are restricted and do not open above the pectoral fin bases. There are two dorsal fins, the first comprised of a single, slim ray, and the second long-based and merging with the caudal fin. The anal fin is single, also merging with the caudal fin. The pelvic fins are thoracic with five rays, 2–3 of which are elongate and not attached to others. The lateral line ends at mid-body.
- Phycidae: This includes hakes and rocklings. There is a single anal fin. There are two dorsal fins, the first either short-based and moderate in height, or comprised of a single elongate, filamentous ray followed by many, very short hair-like rays. There is a single chin barbel, or 2–4 barbels on the snout as well as on the chin. The pelvic fin is normal in shape and length, or with two very elongate rays, often reaching the level of the anus.
- Steindachneriidae: This includes the luminous hake. The body is long, compressed laterally, and tapers to a point. The head is compressed laterally, and the mouth is very large. There are two dorsal fins, the first with one spine and 7–9 rays, the second with 123 or more rays. The anal fin is comprised of 123 to more than 125, very short rays. The first ray of the pelvic fin is elongate and filamentous. The anus is between the pelvic fin rays and is separated from the urogenital opening just anterior to the anal fin. A purplish, striated light organ covers the lower body and sides of head.

Distribution

The distribution of gadiform fishes varies by family, but in general, gadiforms are residents of cool water, therefore occurring throughout the water column in high latitudes, but mainly in deeper layers of tropical waters, where temperatures are lower (a phenomenon known as "tropical submergence"). Members of the gadiforms are primarily marine, but a few freshwater or estuarine species occur. The distribution of each family was summarized in Marshall and Cohen (1973). Bregmacerotids differ somewhat from the rest of the order in their distribution in tropical and subtropical seas. The single euclichthyid species occurs in Australian and New Zealand waters, where it lives near the bottom in deep water.

Gadids are centered in continental shelf waters of the temperate and boreal North Atlantic, although a few members



Examples of larval stages of gadiform fishes: 1. Moridae, *Gadella maraldi*; 2. Macrouridae, *Gadomus* sp.; 3. Macrouridae, *Coryphaenoides* sp.; 4. Muraenolepididae, *Muraenolepis* sp.; 5. Melanonidae, *Melanonus* sp.; 6. Merlucciidae, *Merluccius productus*; 7. Steindachneriidae, *Steindachneria argentea*; 8. Bregmacerotidae, *Bregmaceros mcclellandi*; 9. Gadidae, *Gadus morhua*; 10. Lotidae, *Brosme brosme*; 11. Phycidae, *Urophycis chuss*. (Illustration by Bruce Worden)

have wandered into cool waters of the North Pacific and some species are circumpolar. Three species in *Gadus*, including the Atlantic cod, occur circumboreally, extending into Arctic waters north of Europe, where they are found as deep as 1,640 ft (500 m). *Melanogrammus aeglefinus*, the economically important haddock, is restricted to the North Atlantic where it occurs off the northeastern United States and northern coasts of Europe. *Microgadus* includes the tomcod, a brackish and freshwater species found along the east coast of Canada and the northeastern United States. *Pollachius* contains two species, one of which is restricted to the eastern North Atlantic, the other occurring on both sides of the North Atlantic. *Theragra chalcogramma*, the Alaska pollock, is a North Pacific species that is widely distributed in temperate to boreal waters. Fishes in the family Lotidae are also centered in the North Atlantic, and one genus (*Lota*) has successfully invaded fresh waters of northern Europe and northern North America.

Members of the speciose family Macrouridae (rattails and grenadiers) occur primarily in deep-water habitats throughout the world's oceans (except for the Arctic). Almost all deep oceanic basins contain a macrourid fauna, and it has been estimated that in the Pacific, members of this family comprise the greatest vertebrate biomass between certain depth strata (Cohen et al. 1990). More macrourid species occur in tropical waters than at high latitudes. Several have very restricted ranges, but the deeper-living species are more widely distributed.

The two species in the family Melanonidae are not well-known or often collected. One species is circumantarctic, the other circumglobal in tropical/subtropical waters. Merluccids occur in continental slope and deep-shelf habitats along coastlines throughout the world. The several species in *Merluccius* are found on both sides of the Atlantic Ocean, the eastern Pacific Ocean, and off southern New Zealand. The enigmatic genus *Lyconus* has been found (rarely) in both the North and South Atlantic oceans. One genus (*Macruronus*) is restricted to subantarctic waters.

The family Moridae is found in all oceans. Most species have very restricted ranges, although *Antimora microlepis* occurs in much of the entire North Pacific. Four species in the

family Muraenolepididae all occur in the Southern Ocean, near the bottom in cold-temperate waters. Each species is restricted to waters around capes or groups of islands surrounding Antarctica.

The Phycidae are bottom-living fishes with a center around the coastlines of the North Atlantic, but with a few Southern Hemisphere species. *Gaidropsarus* exhibits a center of abundance in the northeast Atlantic Ocean, but also extends to Japan, New Zealand, and South Africa. *Phycis* contains two species, which are benthopelagic along the eastern North Atlantic Ocean coast. The several species in *Urophycis* are distributed in the western Atlantic Ocean from Canada through Argentina. *Enchelyopus cimbrius* is found on both sides of the North Atlantic, where it occurs along the east coasts of the United States and Canada, the Gulf of Mexico, southern Greenland, Iceland, and the north coasts of Europe. Finally, the monotypic family Steindachneriidae (*Steindachneria argentea*) is restricted to fairly deep waters of the Gulf of Mexico, Caribbean Sea, and continental slope waters off the eastern United States.

Habitat

Habitats occupied by gadiforms vary by family and by genera. Bregmacerotids occur epi- or mesopelagically in open-oceanic waters, extending at times to shallow, coastal habitats. Some have occasionally been found in estuaries. *Euclichthys polynemus*, the sole species in the family Euclichthyidae, occurs benthopelagically in depths of 820–2,625 ft (250–800 m).

Most species in the Gadidae occur demersally (on the bottom) or benthopelagically. Very few (e.g. *Gadiculus argenteus*) are pelagic (live in the water column off the bottom). The demersal species occur over a variety of substrates (rock, sand, mud, gravel, or shell debris), most prefer one over the others, and some undertake seasonal migrations between habitat types. The two species in *Pollachius* are pelagic, and sometimes form large wandering schools that migrate seasonally. The many species in the Macrouridae are found in all oceans, where they occur over very deep bottoms, including the deep ocean basins. The deepest-occurring species occur at greater than 3.7 mi (6,000 m), and few occur shallower than 328 ft (100 m). Melanonids are widely distributed in open ocean meso- and bathypelagic depths between tropical and subantarctic waters.

Most species in the genera *Merluccius* and *Melanonus* occur over continental shelves or upper continental slopes. Favored bottom types occupied by species in the genus *Merluccius* range from sandy to muddy. The ill-known genus *Lyconus* is pelagic and occurs in open waters of the Atlantic Ocean.

Morids are pelagic to benthopelagic, and occur from shallow coastal habitats (rarely including estuarine habitats) to deep oceanic waters. Favored bottom habitats range from soft to hard bottoms, and from sand to mud. Muraenolepidids live near bottom in moderate depths in waters surrounding Antarctica. Phycids are demersal fishes living on a variety of substrates ranging from mud to sand to shell debris. Finally, *Steindachneria argentea* lives in the lower water column over soft bottoms on the deeper parts of the continental shelf and upper continental slope.

Habitat requirements of most gadiforms vary according to their life-history stage or age. It is impossible to propose a generalized model of those varying habitat requirements because each family and each species exhibits its own pattern. For example, within the Phycidae, the white hake, *Urophycis tenuis*, spawns beyond the continental shelf off the northeastern United States, and the fertilized eggs rise into open ocean layers near the surface in an area known as the "Slope Sea." The larvae hatch and develop into a pelagic-juvenile stage, strongly associated with the surface. As they grow they migrate across the entire breadth of the continental shelf toward shore. They arrive in estuaries as small juveniles and spend one season there growing rapidly, finally leaving the estuary at sizes of about 6 in (15.2 cm) at the end of the summer. One- and two-year-olds may remain segregated from older fish by virtue of their occupation of shallower bays and near coastal waters. Subsequently they mingle with the rest of the adult population on deeper parts of the continental shelf, with seasonal migrations into shallower waters. The white hake's range of habitat requirements, therefore, extends from the estuary, across the breadth of the continental shelf, to the upper part of the continental slope, and also includes the entire water column, from surface to bottom (Fahay and Able 1989).

Another phycid, *Urophycis chuss*, the red hake, has very specialized habitat requirements. The fertilized eggs occur in near-surface layers of oceanic waters off the northeastern United States. After hatching, the developing larvae occupy the same general layers. The larvae gradually acquire silvery coloration and go through a pelagic-juvenile stage when they occur epipelagically or neustonically, within a few inches of the surface, often associated with floating weed or debris. After about two months of this pelagic existence, red hakes settle to the ocean bottom and seek shelter in a variety of structured habitats including beds of clam shells, anemone or polychaete tubes, depressions made by fishes or crustaceans, or most frequently, beds of scallops, *Placopecten magellanicus*. The young fishes have been found hiding under scallops, but more frequently they enter into an inquiline association with them whereby they live within the scallops' mantle cavities. The young fish remain in this association through their first winter, finally emerging when they are about 4 in (10.2 cm) long in the spring, and then they remain in coastal or estuarine waters through the next summer. When waters cool in the fall, they join older fish in an offshore migration toward the edge of the continental shelf, where they spend their second winter. Their required habitats, therefore, include the entire water column from surface to bottom, specific beds of invertebrate hosts on the substrate, and the entire breadth of the continental shelf from estuary to shelf edge depending on the season (Able and Fahay 1998).

The Atlantic cod also has habitat requirements specific to its life history stages. The fertilized eggs are pelagic and occur in waters overlying bays, the continental shelf, and important banks and shoals, (e.g. eastern Georges Bank, Grand Banks). Larvae are also pelagic and drift slowly away from spawning areas as they develop. The early juveniles descend to the bottom when they are about 2 in (5.1 cm) long and set-

tle on pebble-gravel deposits on important banks, such as the northeast peak of Georges Bank. After settlement, young fishes appear to favor vegetated habitats (such as eelgrass) in coastal embayments, where they avoid predation by older cod, as well as other predators. After two or three years of segregation from adults, these one- and two-year-olds finally join the adult population. Adults exhibit seasonal movements associated with depth and temperature fluctuations, generally moving into shallower waters during summer and retreating to deeper waters for the winter. Data are available demonstrating habitat preferences based on depth, temperature, and salinity, but surprisingly little is known about bottom types favored. Rocky, pebbly, sandy, and gravelly have all been used to describe cod haunts.

Behavior

In general, gadiform fishes are demersal and highly piscivorus, but there are exceptions to these characterizations. These fishes occur primarily in colder waters, but many exhibit seasonal migrations associated with reproduction or the quest for important prey items. Observations on actual spawning behavior are few, and data on day–night differences in their behavior are also few. Feeding behavior also varies seasonally for many species, with a characteristic pattern involving cessation of feeding activity during spawning seasons.

Feeding ecology and diet

Many gadiform fishes feed on prey items occurring in the substrate, and they are assisted in their search for food by the presence of tactile barbels on their chins. Barbels are well developed in almost all of the gadids, phycids, lotids, macrourids, morids, and muraenolepidids, all of whom feed actively on benthic items. Conversely, the diet of one of the most pelagic of the gadids, the pollock (*Pollachius virens*), consists primarily of euphausiids and Atlantic herring, and its much-reduced barbel reflects this focus on pelagic prey. Certain other pelagic gadiforms, such as the melanonids, bregmacerotids, and *Euclichthys polynemus*, lack chin barbels, and although their food habits are not well studied, it can be assumed that their important diet items are also pelagic.

The phycid hakes *Urophycis chuss* and *U. tenuis* (red hake and white hake, respectively) have similar food habits, although they do not always occur in the same habitats. Both species focus on crustaceans and eat other fishes only secondarily. Annelids, molluscs, and all other prey constitute a minor fraction of their diets. Their feeding behavior also takes advantage of sensitive pelvic fin rays, which are deployed in advance of the fish and aid in the search for prey through their tactile abilities. The Atlantic cod is primarily a piscivore. Among the fishes it consumes, the herring, *Clupea harengus*, is perhaps the most important, but redfish, mackerel, and smaller cod are also important prey items, and diet components are likely to vary between different study sites. Certain Newfoundland studies have found the capelin to be critically important. Cod also eat crabs, and in some studies crustaceans have been identified as more important than fishes. The haddock, *Melanogrammus aeglefinus*, has slightly different food habits than its relative, the cod. Although it focuses on crustaceans as a major dietary component, fishes are unimportant in the remainder of its diet, while polychaetes and echinoderms are secondarily important. The diets of macrourids are highly variable and consist of a wide range of fishes and benthic and pelagic invertebrates. Merlucciids are voracious predators, and the several species of *Merluccius* are highly piscivorous.

Specific information concerning the species that prey on gadiform fishes is lacking for most species. Adults of larger, commercially important species (cod, haddock, etc.) are probably only preyed upon by sharks, billfishes, and other large predators, and their most important predator is undoubtedly man. Young stages of all species, however, face predation by a large number of species, and this plays a large part in determining year-class strength. Some of their predators are larger members of the same species.

Reproductive biology

More is known about reproduction and egg and larval development in the families Gadidae and Merlucciidae, for those two contain commercially important species that have received the most attention. Gadiform fishes, in general, release masses of eggs that are then fertilized externally. Almost all of those eggs are pelagic (although little is known about reproduction in the deep-water species). The Atlantic cod is one of the world's most fecund fishes. A female of 11.0 lb (5 kg) is capable of producing 2.5 million eggs, and larger females can produce more. The haddock is not far behind. A female just under a meter in length can produce close to 2 million eggs. Eggs of gadiforms range from about 0.02 in (0.5 mm) in diameter in some morids and phycids, to about 0.08 in (2.0 mm) in certain gadids and macrourids. The chorion (outer shell) is smooth in most, but it may have a hexagonal pattern in the Macrouridae. Most gadiform eggs have a single, small oil globule, although eggs of the gadids lack an oil globule. Early life history stages are known for fewer than a third of the species described in the Gadiformes, but some descriptions are available for each family. Gadiform larvae exhibit a diverse array of shapes and specializations. According to Fahay and Markle (1984), "There does not seem to be any character unique or diagnostic for young gadiforms. The features of body shape, anus morphology, and pelvic fin development in combination with specific familial characters appear to be the most useful for initial identification. Transformation is gradual and direct with no striking changes in ontogeny." The gut of most gadiform larvae coils early in ontogeny, and combined with a tapering postanal region and rounded head, contributes to an overall tadpole-like appearance. It has not been documented in all gadiform families and is not always easily observed, but very young gadiform larvae have an anus that exits laterally through the finfold rather than at its edge as in most fish larvae. Another characteristic of gadiform larvae is that some secondary caudal rays develop before some primary rays (in forms that have a caudal fin).

Conservation status

The IUCN lists three gadiform species: *Physiculus helenaensis* is categorized as Critically Endangered, and *Gadus*

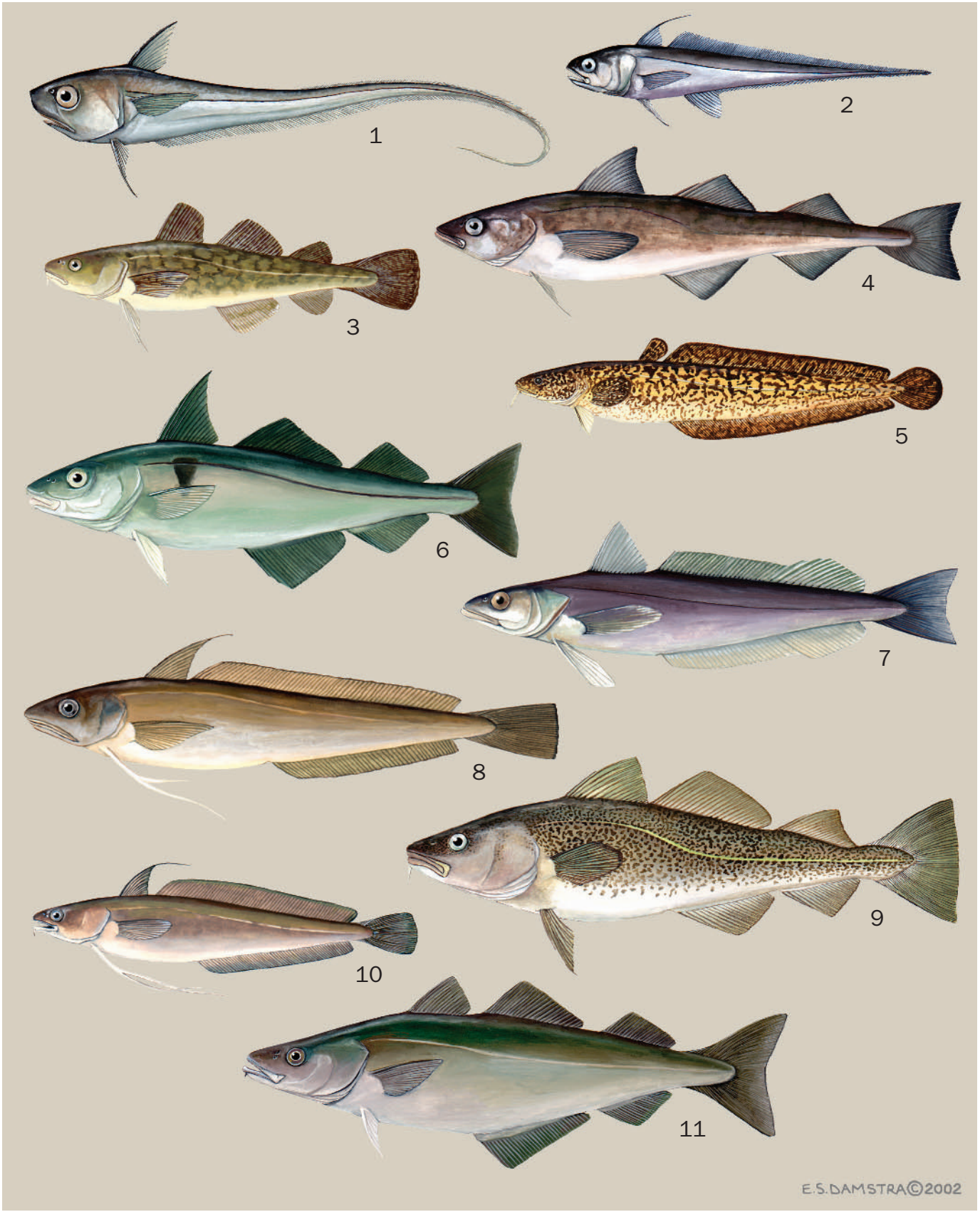
morhua and *Melanogrammus aeglefinus* are categorized as Vulnerable. There are no gadiform fishes listed by the United States as endangered or threatened. However, among the factors threatening the sustainability of viable populations of gadiform fishes, overfishing figures high, especially regarding the Atlantic cod, *Gadus morhua*. In some important areas, for example eastern Canadian provinces, the cod is commercially extinct, meaning its population levels are so low that it can no longer sustain a fishery. The loss of various marine habitats, critically important to the survival of young fishes (as well as older stages), is often cited as contributory to fish populations' declines. For almost all fishes, our knowledge of the critical function of these habitats is lacking or superficial, and increased research in these areas is often cited as necessary for proper management of marine resources.

Significance to humans

Certain gadiforms are among the world's most commercially important fishes. In the late 1980s, for example, some 15,101,665 tn (13,700,000 metric tons [t]), representing fully 17% of the world's landings of marine fishes, were comprised of gadiforms. Of this total, 95% was contributed by the Gadidae (cods and their relatives), followed by the merlucciids, the macrourids, and morids.

The Atlantic cod has been an important fishery for centuries, and this fishery has actually influenced the development of western civilization in countries around the perimeter of the North Atlantic Ocean (Kurlansky 1997). It is said that when John Cabot arrived in Newfoundland waters, supposedly the first European explorer to do so, he was greeted by a well-established fleet of Basque fishermen, who in turn had been fishing for cod in Grand Banks waters for centuries before that. In the days before refrigeration, during the time when the Catholic Church mandated the eating of fish on Fridays and holy days, a good-tasting, lean fish that dried well was in a position to dominate the European markets. The Basques were pioneers and masters both in catching and processing cod and therefore enjoyed a commanding position in the world's economy. Despite the heavy fishing pressure exerted on the cod stocks during past centuries, it sustained a huge fishery until the late 1900s, when increased exploitation, based on increasingly efficient fishing methods (possibly combined with changing environmental trends), finally contributed to the collapse of the cod population. The collapse of the stocks off Labrador and Newfoundland has had particularly devastating and tragic economic consequences in eastern Canada, where the effects have been compared to the Great Depression during the 1930s in the United States.

Other gadiforms are also the basis for valuable fisheries. The Alaska (or walleye) pollock, *Theragra chalcogramma*, contributes more to the world's fisheries than any other demersal fish species, of any family. The total annual landings of this fish in the late 1980s reached 7,389,750 tn (6,703,868 t). The merlucciids (hakes of the genus *Merluccius* and two species of *Macruronus*) were once considered trash fish, but now 11 species are being exploited. In the late 1980s, 2,180,192.1 tn (1,977,837 t) were harvested, making them the second most commercially important family of gadiforms after the Gadidae.



1. Roundnose grenadier (*Coryphaenoides rupestris*); 2. Luminous hake (*Steindachneria argentea*); 3. Atlantic tomcod (*Microgadus tomcod*); 4. Alaska pollock (*Theragra chalcogramma*); 5. Burbot (*Lota lota*); 6. Haddock (*Melanogrammus aeglefinus*); 7. Silver hake (*Merluccius bilinearis*); 8. White hake (*Urophycis tenuis*); 9. Atlantic cod (*Gadus morhua*); 10. Red hake (*Urophycis chuss*); 11. Pollock (*Pollachius virens*). (Illustration by Emily Damstra)

Species accounts

Atlantic cod
Gadus morhua

FAMILY
Gadidae

TAXONOMY
Gadus morhua Linnaeus, 1758, Atlantic Ocean and the coasts of Europe.

OTHER COMMON NAMES
None known.

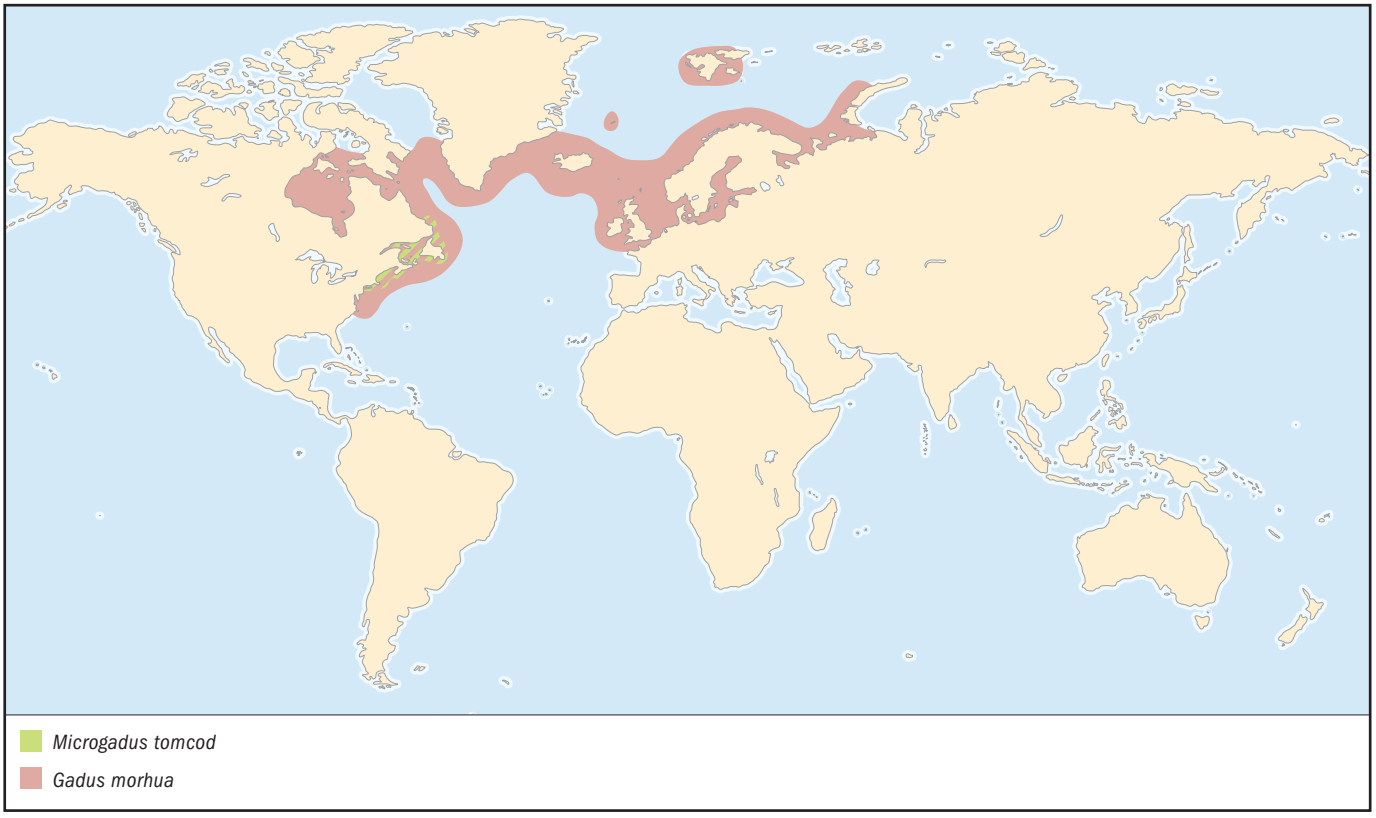
PHYSICAL CHARACTERISTICS
Three separate dorsal fins, two separate anal fins. Dorsal and anal fins touching at their bases or separated by very narrow gaps. Chin barbel present. Pelvic fins sometimes with one elongate ray. Head relatively narrow and long. Snout to base of first dorsal fin length <33% of total length. Overall brownish to greenish gray on upper sides, paler ventrally. Body covered with spots, sometimes vague.

DISTRIBUTION
East coast of North America, north of Cape Hatteras, North Carolina, Hudson Bay, both coasts of southern Greenland, Iceland, coast of Europe from Bay of Biscay to Barents Sea.

HABITAT
Widely distributed in a variety of habitats from close to shore to depths >1,968 ft (600 m), but most common over continental shelf between 492 and 656 ft (150 and 200 m). Mostly demersal, although incursions into water column may coincide with feeding or reproduction. Also found in river mouths from late fall to early winter. Tolerates a wide range of temperatures and salinities, but larger fish generally occur in colder water 32–41°F (0–5°C).

BEHAVIOR
The Atlantic cod is a highly migratory fish. Patterns of migrations differ somewhat between regions. This pattern is associated with reproduction and seasonal temperature change in the Newfoundland stock (Rose 1993). Here, huge schools of cod leave their wintering areas in deep, oceanic waters, and follow tongues of deep, relatively warm, oceanic waters (or highways) across the continental shelf to summer feeding areas nearer to the coast. Spawning occurs in dense concentrations (>1 fish/m^3) as they begin this mass movement, with multiple pairs of spawning fish observed in columns above the mass. As this huge mass migrates inshore, it periodically encounters important prey aggregations (such as capelin or shrimp) and disperses in order to feed. The mass is led by the largest fish (or scouts), and the smallest bring up the rear. After reaching nearshore waters, they turn and move northward along the Newfoundland coast in late summer, then eventually return to their deep-water wintering areas.

Off New England, Atlantic cod typically move into coastal waters during the fall, and then retreat into deeper waters during spring. A slightly different pattern occurs in the Great



South Channel area where they move southwesterly during the fall, spend the winter off southern New England and the Middle Atlantic coast, and then reverse this movement during the spring.

FEEDING ECOLOGY AND DIET
Diet changes with life history stage. The cod is generally omnivorous and voracious. For most ages, feeding occurs in twilight (dawn and dusk), but young fish feed almost continuously. Larvae feed on plankton; juveniles feed on invertebrates, especially small crustaceans; older fish feed on invertebrates and fishes, including young cod. Important diet items are likely to vary between study areas. Herring and capelin are important items in some areas.

REPRODUCTIVE BIOLOGY
Size and age at maturity have declined in recent years, most likely as a response to the fishery harvesting older and larger fish, or to a general decline in the stock biomass due to intense exploitation. A Scotian Shelf study (Beacham 1983) found that median age at maturity declined about 50% from 1959 (when age at 50% maturity was 5.4 years in males; 6.3 years in females) to 1979 (when age at 50% maturity was 2.8 years in both sexes). Median lengths at maturity declined from 20.1 to 15.4 in (51 to 39 cm) in males; 21.3 to 16.5 in (54 to 42 cm) in females. This smaller-and-younger-at-maturity trend continued between 1972 and 1995 in all zones between Georges Bank and Labrador, until presently in United States waters, maturity is reached between 1.7 and 2.3 years (median age) and 12.6 and 16.1 in (32 and 41 cm) (average length). Off the northeastern United States, the distribution of eggs indicates that important spawning occurs over the northeast peak of Georges Bank and around the perimeter of the Gulf of Maine. Reproduction peaks in winter and spring, but continues weakly throughout the year. The North Sea is a major center for reproduction in the eastern Atlantic, where spawning peaks between December and May. Eggs and larvae are pelagic, and juveniles begin descending to the bottom at sizes between 1.0 and 2.4 in (2.5 and 6.0 cm).

CONSERVATION STATUS
The Atlantic cod is listed as Vulnerable by the IUCN. Populations are heavily overexploited by fisheries and are at reduced levels of abundance. Both commercial landings and estimates of spawning stock size are at their lowest levels since 1960. Catch limits are strictly managed, and several important fishing grounds, e.g. portions of Georges Bank, have been closed to all fishing, largely in response to these low levels.

SIGNIFICANCE TO HUMANS
The importance of the Atlantic cod through history can hardly be overemphasized. For the past 1,000 years, the capture, preparation, and distribution of the cod has influenced the development of Western Civilization, especially around the perimeter of the North Atlantic Ocean. The Vikings crossed the Atlantic in pursuit of the cod. The Basques turned the cod into a commercial product in medieval times. Cape Cod was named in honor of the cod in 1602. The cod has actually been the cause of wars between countries, from American colonial times to recent conflicts between Iceland and Great Britain in the twentieth century. Newfoundland was settled by Irish and English natives in the early eighteenth century, largely because of opportunities in the cod fishery. Throughout most of the nineteenth century, this fishery was the most important source of employment and income for people in Newfoundland and much of Eastern Canada. In 1992, the cod population nearly reached a point of commercial extinction in waters off eastern Canada and Newfoundland, and a fishing moratorium was imposed. This moratorium has removed the main source of employment and income for thousands of fishermen from hundreds of small fishing communities and has truly devastated the Canadian economy. ◆

Haddock
Melanogrammus aeglefinus

FAMILY
Gadidae

TAXONOMY
Melanogrammus aeglefinus Linnaeus, 1758, Oceano Europeo.

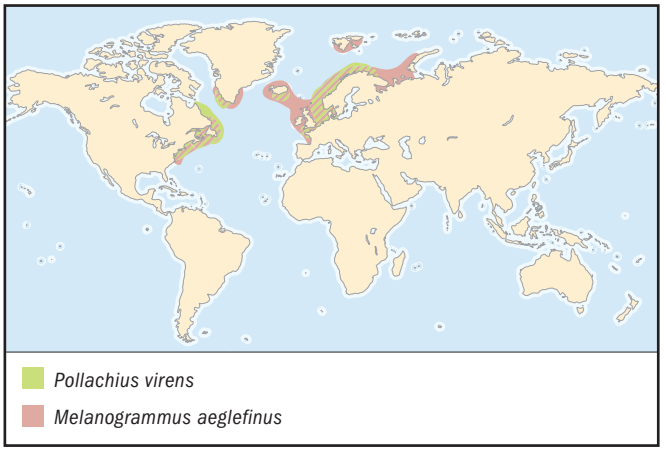
OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Three separate dorsal fins, two separate anal fins. Dorsal and anal fins separated by narrow gaps. Small chin barbel present. Pelvic fins sometimes with one elongate ray. Lateral line dark. A prominent blotch on side over the pectoral fin.

DISTRIBUTION
Eastern North Atlantic from Bay of Biscay to Spitzbergen; Barents Sea; around Iceland and southern tip of Greenland; Western North Atlantic from Labrador to Cape Charles, Virginia. In the western Atlantic, highest abundance occurs over Georges Bank, Scotian Shelf, and southern Grand Bank. The highest concentrations off the United States are associated with the two major stocks located on Georges Bank and in the southwestern Gulf of Maine.

HABITAT
Haddock are most common at depths of 148–443 ft (45–135 m) and temperatures of 36–50°F (2.2–10°C). Substrates preferred include rock, sand, gravel, or broken shell. Gravelly sand and gravel are preferred in the Western Atlantic. Haddock exhibit age-dependent shifts in habitat use, with juveniles occupying shallower water on bank and shoal areas, and larger adults associated with deeper water.

BEHAVIOR
Adult haddock do not undertake long migrations, but seasonal movements occur in the western Gulf of Maine, the Great South Channel, and on the northeast peak of Georges Bank.



FEEDING ECOLOGY AND DIET
Crustaceans, echinoderms, polychaetes, and mollusks are the most important prey items for juveniles and adults combined. Juveniles prey mostly on crustaceans. Other fishes are of minor importance in the haddock's diet.

REPRODUCTIVE BIOLOGY
Spawning occurs between January and June, with peak activity during late March and early April. An average-sized 21.7 in (55 cm) female produces approximately 850,000 eggs, and larger females are capable of producing up to three million eggs annually. Spawning concentrations occur on eastern Georges Bank, to the east of Nantucket Shoals, and along the Maine coast. Growth and maturation rates of haddock have changed significantly over the past 30 to 40 years. During the early 1960s, all females age four and older were fully mature, and approximately 75% of age three females were mature. Presently, growth is more rapid, with haddock reaching 18.9 to 19.7 in (48 to 50 cm) at age three. Nearly all age three and 35% of age two females are mature. Although early maturing fish increase spawning stock biomass, the degree to which these younger fish contribute to reproductive success of the population is uncertain.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN. The spawning stock biomass of Georges Bank haddock declined from 76,000 tn (69,000 t) in 1978 to 12,125 tn (11,000 t) by 1993, and has since increased to 41,900 tn (38,000 t) in 1998. However, spawning stock biomass is presently below the minimum threshold level of 58,400 tn (53,000 t), indicating the stock is in an overfished condition. Observed increases in spawning stock biomass of Georges Bank haddock have resulted from conservation of existing year classes. This is a necessary first step in the stock rebuilding process. Recent research vessel surveys provide indications that the 1998 year class may be the strongest in two decades. If this recruitment is realized, there is a potential for significant stock rebuilding.

SIGNIFICANCE TO HUMANS
An extremely valuable fishery on both sides of the North Atlantic. In 1987, the FAO reported that landings of this species amounted to 439,295 tn (398,522 t), of which total most (400,530 tn; 363,353 t) was taken in the northeastern Atlantic. Leading fishing countries are United Kingdom, Russia, Norway, and Iceland, followed by France, Denmark, and others. Northwest Atlantic landings are dominated by Canada, followed by the United States. ◆

Atlantic tomcod
Microgadus tomcod

FAMILY
Gadidae

TAXONOMY
Microgadus tomcod Walbaum, 1792, Artedi.

OTHER COMMON NAMES
English: Frostfish.

PHYSICAL CHARACTERISTICS
Three separate dorsal fins, two separate anal fins. Dorsal and anal fins separated by gaps and rounded in outline. Chin barbel present. Pelvic fins with one elongate ray. Caudal fin rounded. Olive brown to green dorsally, paler ventrally, with darker mottling on sides.

DISTRIBUTION
Once reported to occur along the coast of North America from Labrador to North Carolina, the tomcod now occurs only as far south as the Hudson River in New York, where it is common.

HABITAT
The tomcod is a coastal fish, ascending rivers into habitats with very low salinities, and living near or on the bottom. It is strictly riverine in the Hudson River, but also can survive landlocked in lakes. Young stages are found in estuaries throughout its range, but not those with limited (or no) freshwater input.

BEHAVIOR
No migrations to offshore waters, but tomcod prefer colder temperatures and move into deeper waters during summer, returning to shallow waters during fall and winter.

FEEDING ECOLOGY AND DIET
Feeds mostly on small crustaceans (especially shrimps and amphipods), worms, small molluscs, squid, and very young fishes.

REPRODUCTIVE BIOLOGY
Tomcod spawning is accomplished during winter, and involves elaborate courtship behavior of small groups. Most egg deposition occurs well upstream, in the lowest salinities available, and eggs are weakly adhesive. In the Hudson River, 93–99% of spawners are young-of-the-year fish approaching their first birthday. Larvae hatch at 0.2–0.24 in (5–6 mm) total length and grow rapidly during their first spring. Growth is then depressed during summer and resumes in the fall.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Tomcod is a popular sport and food fish, mostly in Canada and New England states. In addition to a limited hook and line fishery, tomcod are taken with bag nets, pocket nets, and weirs. ◆

Pollock
Pollachius virens

FAMILY
Gadidae

TAXONOMY
Pollachius virens Linnaeus, 1758, Oceano Europeo.

OTHER COMMON NAMES
English: Coalfish, saithe.

PHYSICAL CHARACTERISTICS
Three separate dorsal fins, two separate anal fins. Dorsal and anal fins separated by narrow gaps. A very small chin barbel present. Lateral line pale. Brownish-green dorsally, slightly paler ventrally. Fins same color as body.

DISTRIBUTION
The pollock occurs on both sides of the North Atlantic. In the western North Atlantic, it is found from the Hudson Strait to Cape Hatteras, North Carolina. In the eastern North Atlantic, from Spitzbergen to Bay of Biscay. Also found in Barents Sea and around Iceland.

HABITAT
The pollock is strongly pelagic and occurs most frequently over depths of 361–590 ft (110–180 m), although its range can vary with food supply and season. Adult fishes occur in temperatures as low as 32°F (0°C), and they do not tolerate temperatures >52°F (11°C). Young stages are known as harbor pollock and are commonly found in bays and estuaries throughout their range.

BEHAVIOR
The pollock is a schooling species and is found throughout the water column, not just near bottom. Pollock engage in short migrations associated with temperature changes or for spawning, but otherwise remain fairly stationary within their range.

FEEDING ECOLOGY AND DIET
The pollock feeds most actively on pelagic prey. Important prey items include euphausiids (especially *Meganyctiphanes norvegica*), fishes, and molluscs (especially the squid *Loligo*). Crustaceans are most important in juveniles' diets. Fishes comprise only 12% of juveniles' diets and 28% of adults' diets.

REPRODUCTIVE BIOLOGY
In the western Atlantic, spawning occurs from September to April with peaks between December and February. Both sexes reach sexual maturity during their third year, at lengths of 19.9 and 18.9 in (50.5 cm and 47.9 cm) in males and females, respectively. Spawners occasionally form huge aggregations. Spawning occurs over hard, rocky bottoms, and activity peaks when temperatures are between 40.1 and 42.8°F (4.5 and 6.0°C). Eggs and larvae develop pelagically, and small pelagic juveniles begin to enter inlets in February and March, when they are <2.0 in (50 mm) long.

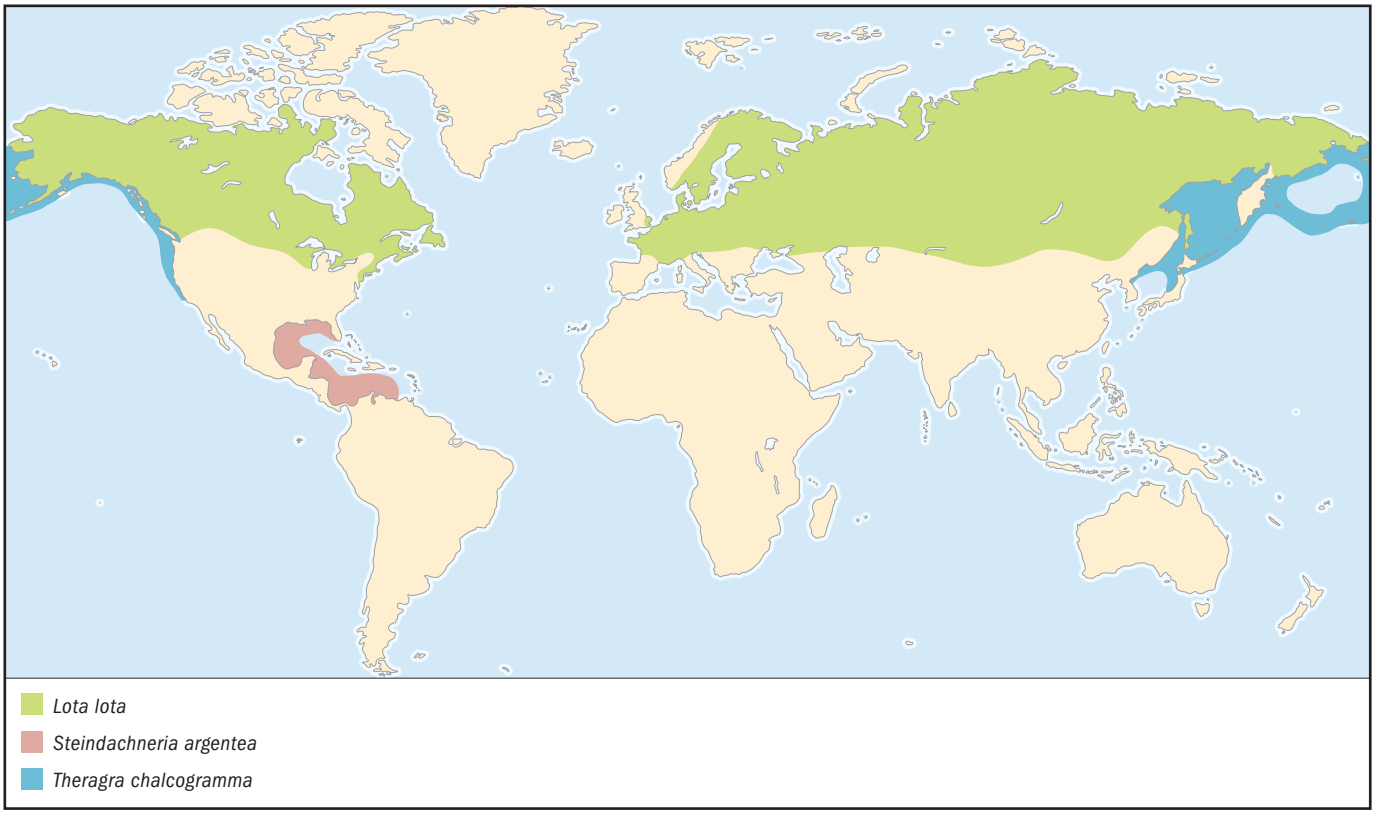
CONSERVATION STATUS
Not listed by the IUCN. Although there are recognized western Atlantic centers of abundance of pollock on the Scotian Shelf, Georges Bank, and Gulf of Maine, tagging studies suggest considerable movement of pollock between these centers and accordingly, pollock from Cape Breton, Nova Scotia, and south continue to be assessed as a single, unit stock by United States scientists. The total nominal catch from this stock, including commercial and recreational, has been steadily declining since 1986, and the 1996 total represents an 82% reduction from 1986 landings. Spawning biomass is increasing, but within the Gulf of Maine, stock abundance and biomass remain low. Overall the stock is considered to be fully exploited, but not yet in an overfished condition.

SIGNIFICANCE TO HUMANS
Pollock is an important commercial species, and it is marketed in several ways: fresh, as chilled fillets, frozen, canned, dried and salted, and in brine. A large percentage of the 1987 total landings 524,680 tn (475,981 t) was landed in the northeast Atlantic by Norway, Iceland, France, Germany, the United Kingdom, and Denmark. Most of the catch in the northwest Atlantic is landed by Canada, the United Kingdom, and France. ◆

Alaska pollock
Theragra chalcogramma

FAMILY
Gadidae

TAXONOMY
Theragra chalcogramma Pallas, 1811, sea of Okhotsk and the shores of Kamchatka.



OTHER COMMON NAMES
English: Walleye pollock.

PHYSICAL CHARACTERISTICS
Three separate dorsal fins, two separate anal fins. Dorsal and anal fins separated by gaps. A very tiny chin barbel present. Pelvic fins sometimes with one ray elongate. Olive green to brown dorsally, silvery on sides, pale ventrally. Often mottled or blotchy.

DISTRIBUTION
Found in temperate and subarctic waters of the Northern Pacific Ocean from Sea of Japan, through Okhotsk Sea, Bering Sea, and Gulf of Alaska, then south to waters off central California. Separate stocks (as many as 12) occur in the North Pacific, including those in the Gulf of Alaska, Aleutian Islands, and Bering Sea.

HABITAT
A schooling fish found on or near the bottom, but also in midwater to near-surface depths. Heaviest catches made at depths between 164 and 984 ft (50 and 300 m).

BEHAVIOR
Alaska pollock perform vertical migrations on a daily basis. Juveniles ascend at night to feed on zooplankton near the surface. Migrations of the entire population associated with spawning and feeding. Alaska pollock follow a circular pattern of migrations in the Bering Sea, moving inshore in the spring to spawn and feed, and offshore to warmer, deeper waters in winter.

FEEDING ECOLOGY AND DIET
Young fish feed on copepod adults and eggs. Adults prey on shrimps, sand lance, and herring off British Columbia; on pink, chum, and coho salmon in Alaskan waters; on mysids, euphausiids, silver smelt, and capelin in Asian waters.

REPRODUCTIVE BIOLOGY
Alaska pollock begin spawning at age two, but ages four and five contribute most to reproduction. Most spawning begins late February in the Bering Sea, March or April in the Gulf of Alaska. Major spawning aggregations are found in Shelikof Strait, Straits of Georgia, Aleutian Basin, and off the Pribilof Islands. Spawning fish form dense schools high in the water column. Fecundity ranges from 37,000 eggs per female to nearly one million off the coast of Canada. In the western Bering Sea, an 11-year-old female can produce 15 million eggs. Eggs are pelagic and occur mostly within 98 ft (30 m) of the surface.

CONSERVATION STATUS
Not listed by the IUCN. Based on estimates of spawning stock biomass and projections into the near future, the Gulf of Alaska stock is not in an overfished condition, nor is it predicted to be.

SIGNIFICANCE TO HUMANS
The Alaska pollock has become an increasingly important human food resource. In the early 1990s, landings of this species were the largest of any demersal fish. The FAO Yearbook of Fishery Statistics for 1987 reported 7,389,750 tn (6,703,868 t) were landed, primarily in the western part of the North Pacific by USSR, Japan, Poland, and Republic of Korea. The largest catches are made over the outer shelf and slope of the eastern Bering Sea, between the Aleutian Islands and the Pribilofs. ◆

Burbot
Lota lota

FAMILY
Lotidae

TAXONOMY
Lota lota Linnaeus, 1758, Europe.

OTHER COMMON NAMES
English: American burbot (Canada), lush (Alaska), lawyer, ling (Canada), eelpout.

PHYSICAL CHARACTERISTICS
Short first dorsal fin followed by long second dorsal fin. Anal fin single, nearly as long-based as second dorsal. Pelvic fins normal, not modified into elongate rays. Well-developed chin barbel. Anterior nostril has barbel-like flap. Color yellow, light tan, to brown, overlain with a blotchy pattern of darker brown or black.

DISTRIBUTION
The burbot occurs in freshwaters of northern North America and Europe and Asia. Occurs farther north than 40° N (to nearly 80° N).

HABITAT
Occurs on the bottoms of lakes and rivers, from depths of 1.6 ft (0.5 m) to more than 755 ft (230 m).

BEHAVIOR
The burbot moves into shallower waters during summer nights. They also move into shallower water to spawn in some parts of their range.

FEEDING ECOLOGY AND DIET
The burbot has been characterized as a voracious predator and night feeder. Young fish feed on insect larvae, crayfish, molluscs and other invertebrates, whereas adults >19.7 in (50 cm) feed almost exclusively on other fishes.

REPRODUCTIVE BIOLOGY
Burbot spawning occurs from November to May, but primarily between January and March in Canada, and December in parts of Russia. Spawning usually occurs under the ice, over sand or gravel substrates, at night, and in shallow water (<9.8 ft [3 m] depth). Eggs are semi buoyant. Fecundity ranges from 45,600 eggs per 13.4-in (34-cm) female to 1,362,077 eggs in a 25.2-in (64-cm) female.

CONSERVATION STATUS
Not listed by the IUCN. The burbot may occur in considerable numbers in many inland lakes, but has declined over past levels in the Great Lakes, where it had been considered a nuisance species.

SIGNIFICANCE TO HUMANS
The burbot is an important competitor for food of other species, such as lake trout and whitefish. It is fished commercially in Finland, Sweden, and the European part of Russia, but it is only moderately important as a commercial species in Canada and Alaska. Often marketed salted or as pet food. ◆

Roundnose grenadier
Coryphaenoides rupestris

FAMILY
Macrouridae

TAXONOMY
Coryphaenoides rupestris Gunnerus, 1765, Trondheim.

OTHER COMMON NAMES
English: Black grenadier, rock grenadier.

PHYSICAL CHARACTERISTICS
Abdominal region (tip of snout to beginning of anal fin) short. Snout broad and rounded. Head broad, soft and deep, with tiny chin barbel. First dorsal fin with two spines and 8–11 rays. Pelvic fin has 7–8 rays, with one elongate. A modified scute-like scale at tip of snout. A wide gap between first and second dorsal fins. Anal fin rays much longer than dorsal fin rays. Color brownish gray, with blackish fins. Reaches greater than a meter in length.

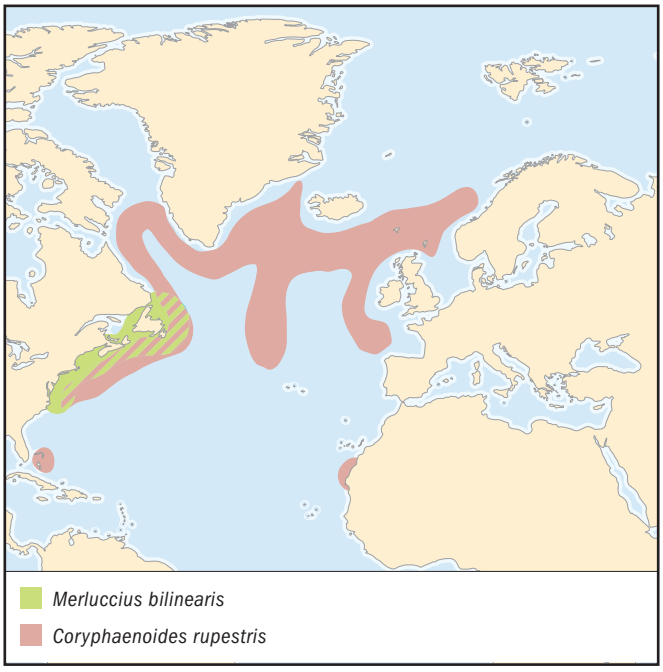
DISTRIBUTION
Occurs in the North Atlantic north of Cape Hatteras, North Carolina to Baffin Island, Greenland, off Iceland and Norway, south to Spain in the Eastern Atlantic. Isolated occurrences off North Africa and Bahamas.

HABITAT
Found between 590 and 7,217 ft (180 and 2,200 m) depth, but concentrated between 1,312 and 3,937 ft (400 and 1,200 m). Adults may be distributed in shallower waters than younger fishes.

BEHAVIOR
Undertakes a post-spawning migration during the winter, back into relatively shallow waters.

FEEDING ECOLOGY AND DIET
Undertakes diurnal, vertical feeding migrations that may take it well off the bottom >3,280 ft (1,000 m). Consumes a variety of fishes and invertebrates, primarily pelagic crustaceans such as shrimps, amphipods, and cumaceans. Also feeds on lanternfishes and cephalapods.

REPRODUCTIVE BIOLOGY
Undertakes spawning migrations during the summer into deeper waters, particularly near Iceland. Females mature at about 23.6 in (60 cm), males at about 15.8 in (40 cm). Fecundity estimates range from 12,000 to 35,500 eggs per female. In some areas, may spawn year-round. The eggs are pelagic, spherical, and 0.091–0.095 in (2.3–2.4 mm) in diameter. Their shell is honeycombed and they contain a single oil globule. The larva has been illustrated by Merrett (1978).



CONSERVATION STATUS
Not listed by the IUCN. A valuable commercial fish species currently facing overexploitation in the North Atlantic.

SIGNIFICANCE TO HUMANS
The roundnose grenadier is a fish with excellent taste and texture. Some 22,000 tn (20,000 t) are landed annually, primarily by fishing fleets from Russia, Germany, and Poland. Its liver is rich in fats and vitamins. ◆

Silver hake
Merluccius bilinearis

FAMILY
Merlucciidae

TAXONOMY
Merluccius bilinearis Mitchill, 1814, New York.

OTHER COMMON NAMES
English: Atlantic whiting.

PHYSICAL CHARACTERISTICS
Genus (hakes) characterized by large head (1/3 to 1/4 of body length), with large, oblique mouth. Lower jaw longer than upper. Two separate dorsal fins, the first short based, high, and triangular, separated from the second, which is long and partially divided by a notch in the midsection. Single anal fin similar in shape to second dorsal. Pelvic fins with seven rays. Silver hake has 16–20 gill rakers on the first arch (cf. 8–11 in closely related *Merluccius albidus*). Color purplish gray dorsally, silvery white lower on sides.

DISTRIBUTION
Occurs on the continental shelf of the northwest Atlantic Ocean from Gulf of St. Lawrence and Grand Banks to offings of North Carolina. Silver hake are most abundant between Nova Scotia and New Jersey. Two stocks have been identified in American waters. One occurs in the Gulf of Maine and northern edge of Georges Bank, the other from the southern edge of Georges Bank to Cape Hatteras, North Carolina.

HABITAT
Silver hake apparently prefer temperatures between 44.6 and 51.8°F (7 and 11°C) in the summer and fall, and 44.6 and 55.4°F (7 and 13°C) in the spring. They occur in depths between 33 and 4,100 ft (10 and 1,250 m), moving into deeper waters during the coldest time of year. Little is known about substrates they prefer, although juveniles 0.6–2.0 in (1.5–5.0 cm) are most abundant on silt-sand bottoms with concentrations of amphipod tubes. During the colder times of year, silver hake become concentrated in deep basins of the Gulf of Maine and along the upper continental slope.

BEHAVIOR
All stocks of silver hake exhibit inshore-offshore migrations associated with temperature changes and availability of important diet items. They are primarily demersal fish, but often move upward in the water column, especially at night, presumably following prey items.

FEEDING ECOLOGY AND DIET
Young silver hake <7.9 in (20 cm) eat mostly crustaceans, such as euphausiids and shrimps. As they grow, they consume increasing proportions of fishes, and adults >13.8 in (35 cm) feed almost exclusively on fishes. Said to be a voracious predator, their diet sometimes includes smaller silver hake.

REPRODUCTIVE BIOLOGY
Major spawning areas include coastal Gulf of Maine, southern Georges Bank, and waters south of Rhode Island. In these areas spawning reaches a peak in June and July. Spawning occurs during late summer off Sable Island Bank in Canadian waters. Females are asynchronous spawners and lay their eggs in several batches through the season. Age and length at maturity have both declined in recent years. In the early 1960s, silver hake reached maturity at two to three years of age and lengths between 11.4 and 13.0 in (29 and 33 cm). By 1989, these figures had declined to 1.6–1.7 years old and 8.8–9.1 in (22.3–23.2 cm), respectively. Another study found that 20% of two-year-olds had reached maturity in 1973, while 80% of two-year-olds had reached maturity in 1990.

CONSERVATION STATUS
Not listed by the IUCN. The decline in size and age at maturity are usually the result of a stock that has been overfished. In both the northern and southern stocks, significant mortality of juvenile silver hake has occurred through discarding in the large mesh and small mesh otter trawl fisheries directed at other species. Annual discard estimates over 1989–1992 ranged from 1,430–11,020 tn (1,300–10,000 t [10 million to 81 million fish]) per year. Excessive discard mortality on juveniles may severely limit opportunities to rebuild either silver hake stock. The southern stock is considered to be in an overfished condition.

SIGNIFICANCE TO HUMANS
The silver hake fishery is important to the United States, Russia, and Cuba. Centers of the fishery are Nova Scotia, Gulf of Maine, and Georges Bank. The total catch in 1987 was 85,950 tn (77,975 t), down from 479,500 tn (435,000 t) in 1973. Silver hake flesh is flaky and good tasting. It is marketed frozen or filleted, and preparation methods include smoking, boiling, and frying. ◆

Red hake
Urophycis chuss

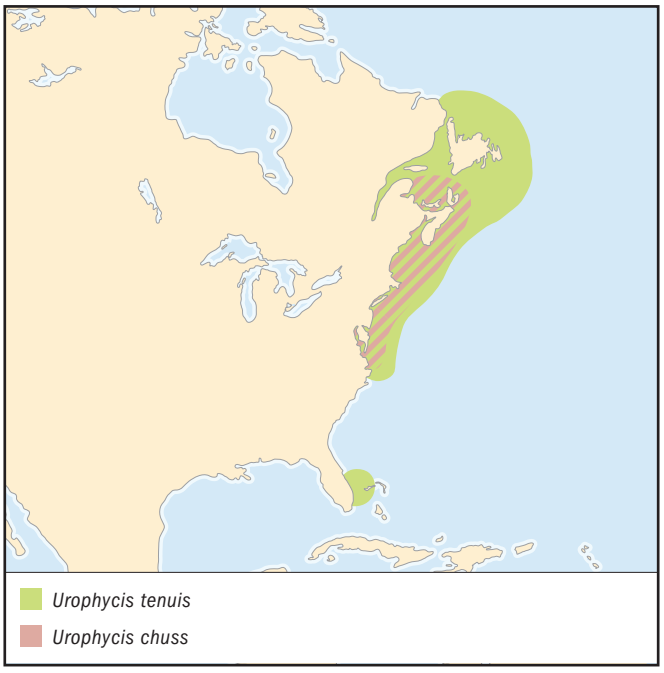
FAMILY
Phycidae

TAXONOMY
Urophycis chuss Walbaum, 1792, Artedi.

OTHER COMMON NAMES
English: Squirrel hake.

PHYSICAL CHARACTERISTICS
Single anal fin. Two dorsal fins, the first short based and moderate in height, with one elongate ray. A single chin barbel. Pelvic fin comprised of two very elongate rays, tip of the longest reaching level of anus. Upper limb of gill raker with three gill rakers; caudal fin with 28–34 rays.

DISTRIBUTION
Western North Atlantic Ocean from Cape Hatteras, North Carolina to Nova Scotia, rarely to Gulf of St. Lawrence. Two



stocks occur off the northeastern United States: a northern stock from the northern slopes of Georges Bank and Gulf of Maine, and a southern stock, from the southern slopes of Georges Bank to North Carolina.

HABITAT
Found on muddy or sandy bottoms, less common on gravelly or hard bottoms. Adults found between 16.4 and >984 ft (5 and >300 m), but some seasonal migrations take place. Early settled juveniles live in an inquiline association with sea scallops, *Placopecten magellanicus*, or other structured habitats, after which they remain in relatively shallow coastal waters until their second year. Thereafter, they are most common in depths <328 ft (100 m) in warmer months, >328 ft (100 m) in colder months.

BEHAVIOR
Red hake migrate seasonally in reaction to changing temperatures. During summer, they are quite common in nearshore bays and estuaries in New England. During the winter, they migrate into deeper waters.

FEEDING ECOLOGY AND DIET
Hakes use their pelvic fin rays as sensory organs to find food (Bardach and Case 1965). Juveniles leave their shelters at night and prey on small benthic organisms such as crustaceans. Adults also prey on crustaceans, but consume a wide variety of fish and squid as well.

REPRODUCTIVE BIOLOGY
Spawning occurs spring through fall off the coast of northeastern United States, but may be restricted to mid-summer in the Gulf of Maine. Eggs and larvae develop pelagically, and the larvae transform into a specialized pelagic–juvenile stage that is highly neustonic (lives very near the surface), often gathering around floating debris. They settle to the bottom at sizes of 1.4–1.6 in (35–40 mm).

CONSERVATION STATUS
Not listed by the IUCN. During the early 1960s, total landings from both stocks (northern and southern) peaked at 125,220 tn (113,600 t) in 1966. Annual landings then declined

sharply to only 14,220 tn (12,900 t) in 1970, increased again to 84,220 tn (76,400 t) in 1972, and then have declined steadily since. Red hake landings averaged only 1,870 tn (1,700 t) per year during 1990–1999, a decline of over 40% from the 1980–1989 average. Red hake landings in 1999 were well below historic levels. Despite these declines, neither stock is presently considered to be in an overfished condition, and recruitment of younger fish appears to be strong.

SIGNIFICANCE TO HUMANS
A variable constituent of the United States and Canadian trawl fisheries. Large fish marketed fresh or frozen, and small fishes sometimes sold for animal feeds. ◆

White hake
Urophycis tenuis

FAMILY
Phycidae

TAXONOMY
Urophycis tenuis Mitchill, 1814, New York.

OTHER COMMON NAMES
English: Mud hake (Canada).

PHYSICAL CHARACTERISTICS
Single anal fin. Two dorsal fins, the first short based and moderate in height, with one elongate ray. A single-chin barbel. Pelvic fin comprised of two very elongate rays, not quite reaching level of anus. Upper limb of gill raker with two gill rakers; caudal fin with 33–39 rays.

DISTRIBUTION
Most commonly from Newfoundland to Cape Hatteras, North Carolina, as far south as Florida in deeper water and around the coasts of Iceland.

HABITAT
Soft, muddy bottoms of the outer continental shelf and upper continental slope. Most occur deeper than 656 ft (200 m). Also found in deeper basins in the Gulf of Maine and submarine canyons along the edge of the continental shelf. Juveniles depend on estuaries during their first spring and summer, where they are common in eel grass beds and other structured habitats.

BEHAVIOR
Young white hake engage in sand-hiding behavior, whereby they bury themselves in sand with only their heads protruding. The entire population typically moves into deeper waters in the fall, although the largest sizes occur in depths of 656 ft (200 m) and deeper and move very little, if at all.

FEEDING ECOLOGY AND DIET
Juveniles feed on polychaetes, shrimps, and other crustaceans. Adults also feed on crustaceans, but augment their diet with fishes, including juvenile white hake.

REPRODUCTIVE BIOLOGY
Spawning occurs in early spring off the northeastern United States, with a separate spawning event during summer over the Scotian Shelf and Gulf of St. Lawrence (Able and Fahay 1998). Larvae develop into a silvery pelagic–juvenile stage that is strongly associated with the ocean surface. These soon migrate into estuaries, where they settle to their first bottom stage, and remain through the summer.

CONSERVATION STATUS
Not listed by the IUCN. Total landings of white hake increased from about 1,102 tn (1,000 t) during the late 1960s to 9,150 tn (8,300 t) in 1985. Landings then declined to 5,622 tn (5,100 t) in 1989, rose sharply to 10,582 tn (9,600 t) in 1992, and have since steadily declined to levels not seen since the early 1970s. Total landings in 1998 were 2,866 tn (2,600 t), a 30% decline from 1996. Results of the most recent assessment indicate the Gulf of Maine–Georges Bank white hake stock is in an overfished condition.

SIGNIFICANCE TO HUMANS
Since 1968, the United States fishery has accounted for approximately 90% of the Gulf of Maine–Georges Bank white hake catch, but Canadian fishermen also land significant amounts from Newfoundland and northern Gulf of Maine. Larger fish are marketed fresh or as frozen fillets. Smaller fish are sometimes used for animal feed. ◆

Luminous hake
Steindachneria argentea

FAMILY
Steindachneriidae

TAXONOMY
Steindachneria argentea Goode and Bean, 1896, off Mississippi River delta.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body long, compressed, tapering to a fine point and tiny caudal fin. Anus separated from urogenital opening, the former situated between the pelvic fin bases, the latter just ahead of the anal fin. A light organ present on the ventral part of body and sides of head, appearing as purplish, striated area. First dorsal fin has one spine and 7–9 rays; second dorsal and anal fins each has more than 123 rays. Anterior portion of anal fin elevated, containing 10–12 rays. Pectoral fin has 14–17 rays. First ray of pelvic fin filamentous. Body silvery, upper part somewhat brownish, belly purplish.

DISTRIBUTION
Found in the central western Atlantic Ocean and off the East Coast of the United States, Gulf of Mexico, and Caribbean Sea as far as Venezuela.

HABITAT
Occurs on outer part of continental shelf and upper continental slope, usually over soft bottoms.

BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Unknown.

REPRODUCTIVE BIOLOGY
Eggs of this species are undescribed. The larvae are pelagic and are uncommonly collected in the Gulf of Mexico. They have large heads and large eyes, and the pectoral fins are somewhat stalked as they develop. The striated luminous organ begins to develop in larvae as small as 0.9 in (24.0 mm), when fin

rays are completely formed. The anus and urogenital opening initially are found together, but the anus migrates forward with development.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
No fishery is directed at this species, although large quantities are sometimes landed between depths of 1,300 and 1,640 ft (400 and 500 m) in the northern Gulf of Mexico. ◆

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Michael P. Fahay

Batrachoidiformes
(Toadfishes)

Class Actinopterygii
Order Batrachoidiformes
Number of families 1

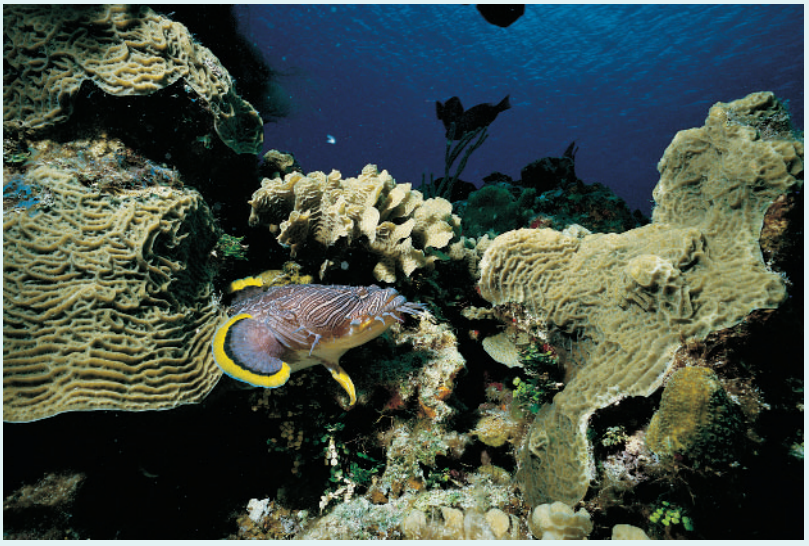


Photo: A splendid coral toadfish (*Sanopus splendidus*) near Cozumel, Mexico. Its striking appearance sets it apart from the other toadfishes. (Photo by J. W. Mowbray/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The family Batrachoididae is the only family in the order Batrachoidiformes, and is thought to be most closely related to the fishes in the order Lophiiformes containing the goosefishes, frogfishes, and deepsea anglers. It has been divided into three subfamilies: Porichthyinae (*Porichthys*, 14 species and *Aphos*, 1 species) and Thalassophryninae (*Daector*, 5 species and *Thalassophryne*, 6 species) are the most derived and are restricted to the New World; Batrachoidinae containing at least 16 genera (including *Opsanus* and *Sanopus*) and about 51 species occur worldwide.

Physical characteristics

Toadfishes are small- to medium-sized fishes with a broad, flattened head and a wide mouth that usually has barbels and/or fleshy flaps around it. The eyes are on top of the head and directed upwards. The pelvic fins are forward, in front of the pectoral fins, and have one spine and three soft rays. There are two separate dorsal fins, the first with two or three spines, and the second is long with 15 to 25 soft rays. The anal fin is somewhat shorter than the second dorsal fin. The pectoral fins are large with a broad base. The gill openings are small and are restricted to the sides of the body. Species of *Porichthys* have photophores (light organs) along their sides and ventral surface. Species in the subfamily Thalassophryninae have hollow, venomous spines in their first dorsal fin and opercles. *Bifax lacinia* has a flap with an eye spot at the end of the maxilla on each side of the mouth.

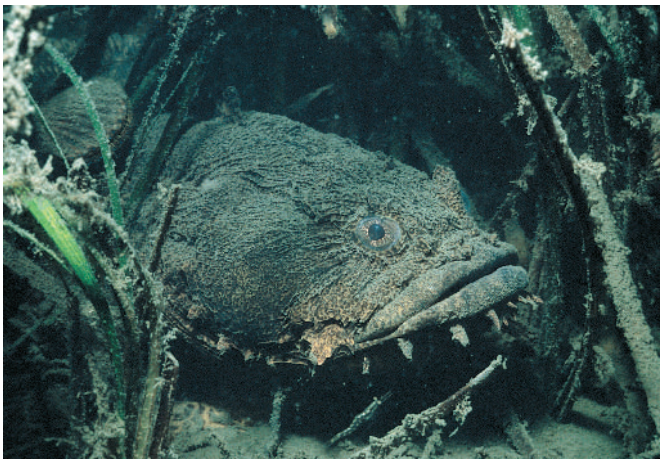
Toadfishes usually are rather drab colored, often brownish with darker saddles, bars, or spots; however, some species in the Atlantic genus *Sanopus* are brightly colored. Maximum size of species ranges from 2.2 in (56 mm) to at least 20.1 in (510 mm) standard length.

Distribution

Worldwide between about 51° N and 45° S along continents in marine and brackish waters, occasionally entering rivers. Several freshwater species in South America.

In the New World Pacific Ocean: the genus *Porichthys* occurs from southeast Alaska south to Ecuador; *Aphos* from Peru south to Chile; *Daector* from Costa Rica to Peru; and *Batrachoides* from Mexico to Peru. In the New World Atlantic Ocean: *Porichthys* occurs from Virginia south to Argentina; *Opsanus* from Massachusetts south to Belize; *Sanopus* from Yucatan, Mexico to Panama; *Triathalassothia* in Belize, Honduras, and Argentina; *Amphichthys* from Panama to Brazil; *Thalassophryne* from Panama to Uruguay. Species of *Daector*,

An oyster toadfish (*Opsanus tau*) resting on the ocean floor. It makes a "grunting" sound when caught. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)



The oyster toadfish (*Opsanus tau*) has been used in studies of insulin and diabetes, drug metabolism, hearing, dizziness and motion sickness. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

Thalassophryne, and *Potamobatrachus* occur in freshwater in South America.

In the eastern Atlantic Ocean *Batrachoides*, *Halobatrachus*, *Perulibatrachus*, and *Chatrabus* occur along the African coast. South Africa has several genera: *Chatrabus*, *Batrichthys*, and *Austrobatrachus*. *Barchatus* is found in the Red Sea and adjacent areas, *Bifax* in the Gulf of Oman as well as *Austrobatrachus*, which ranges to India. *Allenbatrachus* ranges from India through the Indo-Australian archipelago to the Philippines and north to Thailand. Toadfishes have not been recorded from Taiwan or Japan. The genus *Halophryne* occurs on the west, north, and east costs of Australia, and north to the Philippine Islands, and *Batrachomoeus* has the same range in Australia and ranges north through the Indo-Australian archipelago to Vietnam.

Habitat

Toadfishes rest on and bury in the substrata and are found from the shoreline down to deep water, at least to 1,200 ft (366 m). They occur in full-strength sea water, brackish water, and also freshwater. Their usual cryptic coloration allows them to blend with the subtrata where they can function as ambush predators. The species in the genus *Sanopus* typically live in sand depressions under coral heads.

Behavior

Toadfishes are known for their sound production resulting from the contraction of muscles on the swim bladder. Both males and females produce agonistic grunts, whereas only males make longer courtship calls, "boat whistles," or "hums."

Feeding ecology and diet

In addition to being ambush predators, toadfishes also move about feeding on invertebrates, mostly crabs, shrimps, mollusks, sea urchins, and fishes, and others take planktonic organisms from the water column.

Reproductive biology

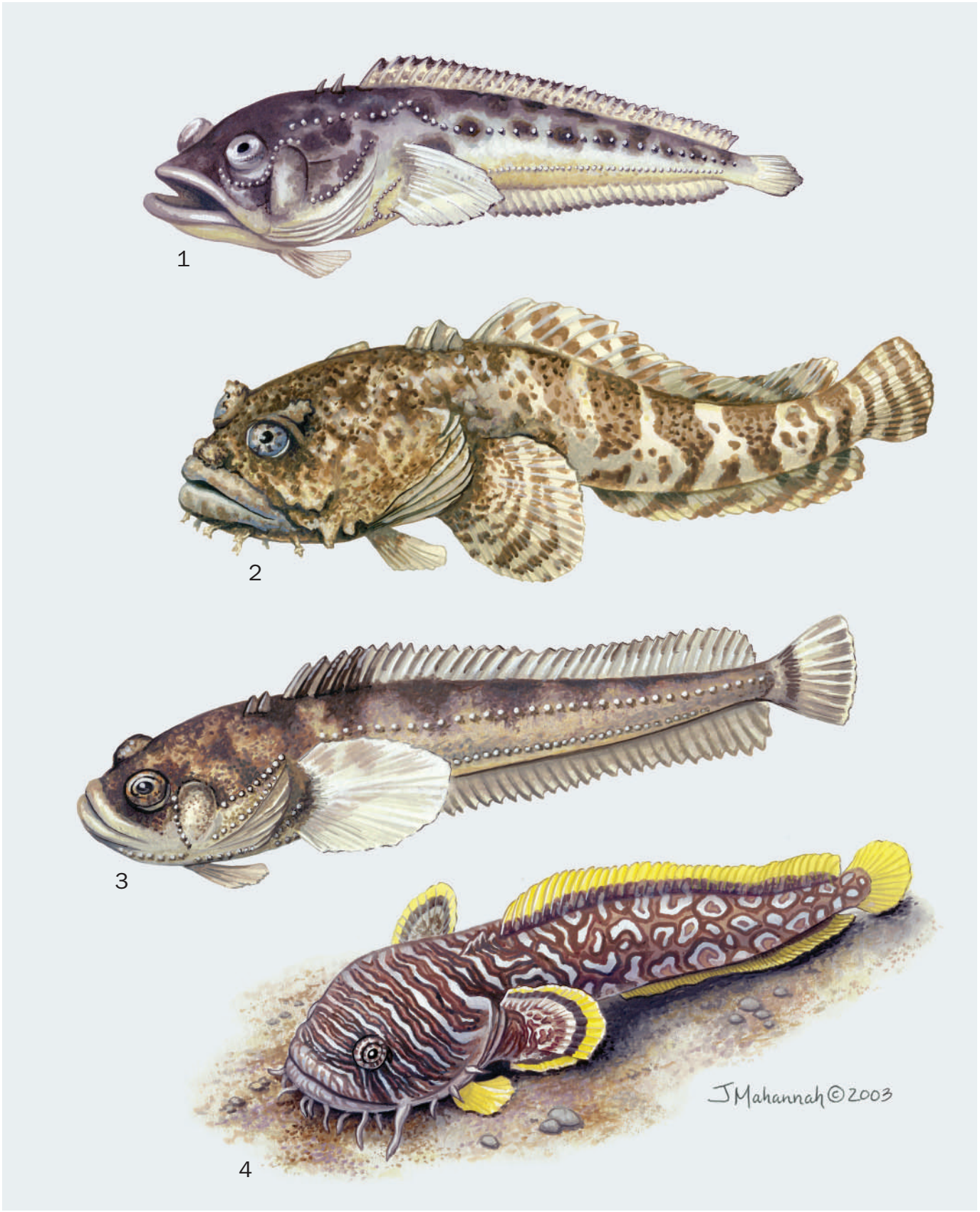
Males prepare nests, usually in a cavity under a rock or shell, including objects discarded by humans such as cans or bottles. Males attract females by vocalizations, and then females lay large, adhesive eggs and leave the area. Males guard and fan the eggs until after hatching. The young may remain in the nest after hatching, still attached to the nest surface and even after free swimming. The plainfin midshipman has two types of males, larger nest holding ones and smaller sneaker males that dart into nests attempting to fertilize eggs of a nesting pair.

Conservation status

The IUCN lists five species of toadfishes as Vulnerable—the Cotuero toadfish (*Batrachoides manglae*), the whitespotted toadfish (*Sanopus astrifer*), the whitelined toadfish (*S. greenfieldorum*), the reticulated toadfish (*S. reticulatus*), and the splendid coral toadfish (*S. splendidus*). A number of species appear to have very limited distributions.

Significance to humans

Larger toadfish species are eaten, although there is no specific fishery for them. Species in the genus *Allenbatrachus* are occasionally collected and sold in the aquarium trade as freshwater fishes. Species in the genera *Opsanus* and *Porichthys* are used in laboratory studies. Venomous toadfishes in the subfamily Thalassophryninae can inflict pain if handled.



1. Atlantic midshipman (*Porichthys plectrodon*); 2. Oyster toadfish (*Opsanus tau*); 3. Plainfin midshipman (*Porichthys notatus*); 4. Splendid coral toadfish (*Sanopus splendidus*). (Illustration by Jacqueline Mahannah)

Species accounts

Oyster toadfish
Opsanus tau

FAMILY
Batrachoididae

TAXONOMY
Gadus tau Linnaeus, 1766, Carolina, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The maximum size is 15 in (381 mm) standard length. There are three dorsal-fin spines, a body lacking scales, and a single subopercular spine. The inner surface of the pectoral fins has discrete glands between the upper rays, and the pectoral fin with an axillary pore behind it. The second dorsal fin has 23–27 soft rays, and the anal fin has 19–23 soft rays. The tongue, gill arches, roof of mouth and inner surface of the gill covers are light, not black, and the background color of the body is dark with no spots. The pectoral fin has definite cross bars.

DISTRIBUTION
Atlantic coast of the United States, from Maine to Miami, Florida.

HABITAT
Usually found over rock, sand, or mud, and oyster shell bottoms, often most abundant in estuaries.

BEHAVIOR
This species makes a grunting noise by rubbing muscles across the swim bladder. Males use a boat-whistle call to attract females to nesting sites.

FEEDING ECOLOGY AND DIET
Feeds mainly on small crabs and other crustaceans.

REPRODUCTIVE BIOLOGY
Males establish nesting sites from April through October. Reproductive behavior typical of the family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Generally considered a nuisance when caught by fishers, but used as an experimental animal for studies involving insulin and diabetes, drug metabolism, hearing, dizziness, and motion sickness. ◆

Plainfin midshipman
Porichthys notatus

FAMILY
Batrachoididae

TAXONOMY
Porichthys notatus Girard, 1854, San Francisco, California, United States.

OTHER COMMON NAMES
English: Singing fish, canary bird fish.

PHYSICAL CHARACTERISTICS
The maximum size is 15 in (380 mm) standard length. There are two spines in the first dorsal fin, and the second dorsal and anal fins are long. There are rows of photophores on the head and body, and those on the underside of the head are V-shaped.

DISTRIBUTION
Southeast Alaska to Baja, California, Mexico.

HABITAT
Usually buried in soft bottom, mud, or sand, but can be found in rocky intertidal areas during breeding season.

BEHAVIOR
Like other family members it produces sound, making grunts and a hum that is a mating call. It has been demonstrated that the photophores can be used as a countershading mechanism to hide the midshipman from predators while it is foraging in the water column at night.

FEEDING ECOLOGY AND DIET
A nocturnal species that is partially buried during the day but at night rises into the water column to feed on planktonic organisms. It has been suggested that its photophores help illuminate food items. It also can function as an ambush predator, taking crustaceans and fishes while buried.

REPRODUCTIVE BIOLOGY
Males establish nests under objects and attract females by humming. Two kinds of males are present, larger nest-holding ones and smaller sneaker males that dart into nests attempting to fertilize eggs of a nesting pair. There have been reports that the photophores also are involved in mating behavior.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The humming of breeding males bothers persons living in houseboats. It is used as a laboratory animal and is an important food item for seals and sea lions. ◆

Atlantic midshipman
Porichthys plectrodon

FAMILY
Batrachoididae

TAXONOMY
Porichthys plectrodon Jordan and Gilbert, 1882, Galveston, Texas, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The maximum size is 8.6 in (218 mm) standard length. There are two spines in the first dorsal fin, and the second dorsal and anal fins are long. There are rows of photophores on the head and body, and those on the underside of the head are U-shaped.

DISTRIBUTION
Cape Henry, Virginia south to northern Brazil, including the Gulf of Mexico and the Caribbean Sea.

HABITAT
Prefers mud bottoms where it buries itself during the day

BEHAVIOR
It produces both aggressive and mating vocalizations. Photophores may be used as a countershading mechanism to avoid predators while foraging in the water column at night.

FEEDING ECOLOGY AND DIET.
Although some benthic invertebrates and fishes have been found in their stomachs, most of the food consists of planktonic crustaceans and larval fishes taken at night while foraging in the water column.

REPRODUCTIVE BIOLOGY
It moves from deeper water into shallow bays and spawns in the spring and summer. The reproductive behavior is typical of the family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Used as an experimental animal. ◆

Splendid coral toadfish
Sanopus splendidus

FAMILY
Batrachoididae

TAXONOMY
Sanopus splendidus Collette, Starck, and Phillips, 1974, Cozumel Island, Mexico.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The maximum size is 9.9 in (252 mm) standard length. There are three dorsal-fin spines; a single subopercular spine; no scales; no glands between the upper rays of the inner surface of pectoral fins; and an axillary pore present. All fins are bordered with black and orange-yellow.

DISTRIBUTION
Known only from off Cozumel Island, Quintana Roo, Mexico.

HABITAT
Usually found in sand depressions under coral heads.

BEHAVIOR
Not known.

FEEDING ECOLOGY AND DIET
An ambush predator feeding on small fishes and gastropods.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN. It is known only from off Cozumel Island and thus is potentially at risk.

SIGNIFICANCE TO HUMANS
Commonly photographed by scuba divers. ◆

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David W. Greenfield, PhD

Lophiiformes
(*Anglerfishes*)

Class Actinopterygii
Order Lophiiformes
Number of families 18

Photo: A frogfish (*Antennarius* sp.) eating a fish. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The anglerfishes (order Lophiiformes) are a remarkable assemblage of approximately 65 genera and nearly 300 species of curious and wonderfully bizarre fishes. Lophiiformes is one of six orders that make up the euteleostean superorder Paracanthopterygii. Of the six paracanthopterygian orders, the toadfishes (order Batrachoidiformes) are considered to be most closely related to the anglerfishes. The fossil record extends back to the Eocene, with representatives from the families Antennariidae and Lophiidae having been found in Eocene formations of Italy.

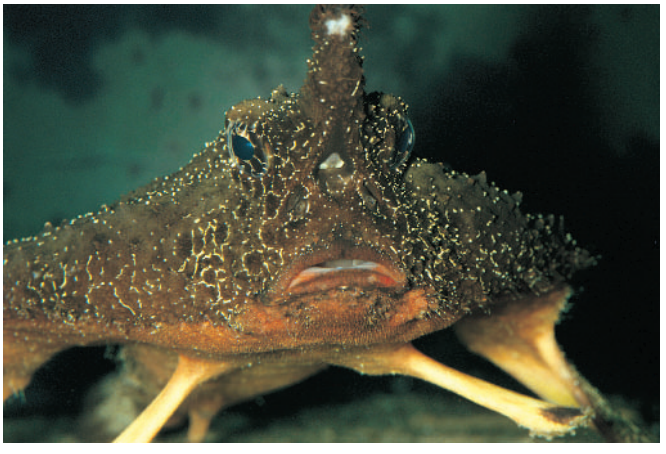
Pietsch and Grobecker recognized 18 lophiiform families and divided them among five suborders. In phylogenetic order and from most primitive to most dervied, they are: Lophioidei (containing only one family, Lophiidae, the monkfishes), Antennarioidei (four families, the frogfishes), Chaunacoidei (one family, Chaunacidae, the sea toads or coffinfishes), Ogcocephaloidei (one family, the batfishes), and Ceratioidei (11 families, the bathypelagic anglerfishes).

Physical characteristics

The anglerfishes share two very conspicuous derived characters (synapomorphies). (1) The anterior portion of the spinous dorsal fin has migrated forward to a position on the anterior surface of the head, just behind the snout. The first dorsal fin spine has been modified further to serve as an angling apparatus (illicium), by loosing its membranous connection to the other cephalic dorsal fin spines and acquiring a distal bait or lure (esca) to help attract prey. (2) The bases of the pectoral fins (radials) have become greatly elongated so that the pectoral fins appear to be at the end of long, jointed arms. The number of pectoral radials has been reduced to between two and five. Additional lophiiform synapomorphies are gill openings that are reduced in size and, in all but the most primitive lophioids, located posterior to the pectoral fin base; five or six branchiostegal rays; absent ribs; and first vertebra fused to the neurocranium. Anglerfishes are very diverse in both color and size; this order ranges from a few inches to approximately 6.6 ft (2 m) in length.

Distribution

Anglerfishes are worldwide in distribution. With the exception of one antennariid (frogfish) species that has been known to enter freshwater, they are exclusively marine, and most species occur in deep water.



The batfish (*Ogcocephalus* sp.) "walks" along the bottom on limb-like fins. A "lure" is located below the base of the rostrum. (Photo by David M. Schleser/Nature's Images, Inc/Photo Researchers, Inc. Reproduced by permission.)

A longlure frogfish (*Antennarius multiocellatus*) extending its lure to attract a fish. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

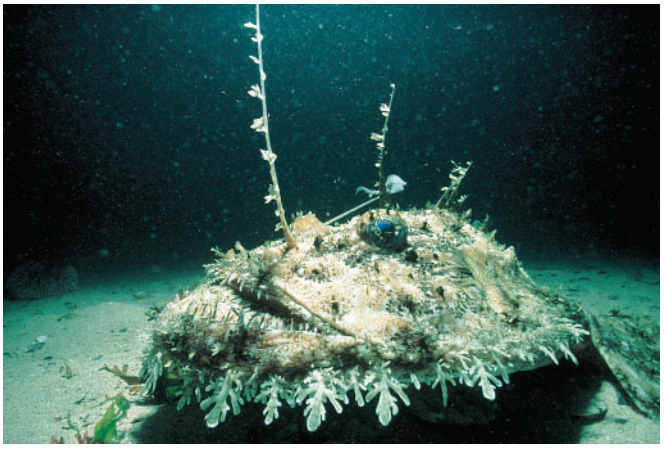
Habitat

Most anglerfishes occur in deep oceanic waters. The ceratioid anglerfishes are midwater fishes, inhabiting primarily the mesopelagic and bathypelagic zones. Most other anglerfishes are benthic and occur in the waters of the outer continental shelf and continental slope. A few lophioids enter the shallows at high latitudes, and many antennarioids occur in coral reef or other shallow habitats in tropical and warm temperate waters.

Behavior

Most knowledge of anglerfish behavior is associated with the specialized adaptations that have made them such effective and successful ambush predators. Most important among them are the angling apparatus and the functional morphological features of the feeding mechanism. These adaptations, along with certain reproductive adaptations, have made the anglerfish among the most successful predators in the deep sea.

The angling apparatus (illicium) is derived from the anteriormost spine in the dorsal fin. The illicium and second dorsal fin spine (if present) articulate with a single, enlarged pterygiophore. The illicium has a rather elaborate set of associated muscles, which allows the angler to move the spine rapidly, thus thrashing the bait (esca) vigorously above or in front of the mouth. In some anglerfishes the bait may be a simple bulb or clublike structure, but in others it can be quite



An angler (*Lophius piscatorius*) resting on the sandy bed of the Atlantic Ocean near Brittany, France. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

An anglerfish "angling" with lure for catching prey. (Illustration by Joseph E. Trumpey)

elaborate. In many deep-sea species, the esca is bioluminescent, while in forms that live in sunlit regions, it may be an elaborate fleshy structure, occasionally resembling a small, shrimplike crustacean in some lophiid species or even a small fish in one species of antennariid.

The mouth in most anglerfishes is cavernous, and in many species it is lined with long, sharp, thin, depressible teeth. The functional morphological features associated with the anglerfish feeding apparatus are quite fascinating. Like many derived teleostean fishes, anglerfishes are "gape-and-suck" feeders. Many anglerfishes, however, have a greatly elongated and highly mobile suspensorium, or hyopalatine arch (the portion of the skull that supports the lower jaw). This feature serves to permit swallowing of very large prey and allows the volume of the buccal cavity to increase to a much greater extent than in other fishes, which results in much greater negative pressure or suction when the mouth is opened rapidly.

Not only can anglerfishes create much greater negative pressure when opening the mouth and expanding the buccal cavity, but they appear to be capable of doing so much more rapidly than other fishes. Pietsch and Grobecker used high-speed cinematography (800 and 1,000 frames/second) to study the functional morphological characteristics of the feeding apparatus in antennariid anglerfishes. They showed that maximum oral expansion and subsequent prey engulfment may occur in as little as four milliseconds, and the average speed for three species of *Antennarius* was seven milliseconds. For comparison, this takes 40 milliseconds in the European perch (*Perca fluviatilis*), 16 milliseconds in the freshwater butterflyfish (*Pantodon buchholzi*), and 15 milliseconds in the stonefish (*Synanceia verrucosa*).

During typical ambush feeding, the anglerfish remains motionless (either on the bottom or in the water column, depending on the family) until suitable prey is detected. Many benthic anglerfishes (e.g., antennariids and lophiids) are capable of remarkable cryptic coloration, whereas the midwater forms are usually very dark brown or black (cryptic in a pelagic environment with little or no light). Upon sensing prey, the angler brings the illicium into play, attempting to attract the prey to within reach (aggressive mimicry). When

A sargassumfish (*Histrio histrio*) floating in a sargassum mat at the ocean surface. (Illustration by Joseph E. Trumpey)

the prey reaches the strike zone, the mouth of the angler opens rapidly, and the buccal cavity expands greatly, creating a strong suction that draws in the prey.

Feeding ecology and diet

Anglerfishes feed primarily upon nekton, especially fishes and other nektonic organisms that probably are attracted by angling apparatus. Batfishes are one of the few groups of anglerfishes that feed primarily on benthic invertebrates. There is evidence suggesting that various kinds of anglerfishes—including large species—are consumed by larger predatory fishes such as sharks.

Reproductive biology

Very little is known about the reproductive biology and early life history of most anglerfishes, but it would appear that the early larval stages of all anglerfishes are pelagic, and thus meroplanktonic. One adaptation that does appear to be common to all anglerfishes is the acquisition of sexual dimorphism in the size and structure of the olfactory organs. This appears to be associated with the production of species-specific pheromones by the females, which attract the males during the breeding season. What little else is known about the reproductive biology of these fishes is restricted primarily to the families Lophiidae, Antennariidae, and a few ceratioid families; within these families, knowledge is likewise restricted to very few species.

A warty frogfish (*Antennarius maculatus*) near a brown sponge and the lava sand of the Lembeh Strait, near Indonesia. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Early life-history stages have been described for a few of the 25 species of lophiid anglerfishes (*Lophius americanus*, *L. budegassa*, and *L. piscatorius*). Larvae of only four of the 41 antennariid species have been described, but only *Antennarius striatus* and *Histrio histrio* are reasonably well known.

In the case of all anglerfishes from which eggs have been identified, eggs are released from the female embedded in a long, bouyant, ribbonlike mucoid veil. This is known to reach a length of 39.4 ft (12 m) and a width of 5 ft (1.5 m) and has been estimated to contain more than 1.3 million eggs in one large lophiid anglerfish species (*L. americanus*). The pigmentation of the embryos imparts a dark hue to the veil, and they are so conspicuous as they float at the surface of the sea that they have long been known to commercial fishermen. In anglerfishes in which the larvae have been identified, the larvae pass through a planktonic stage before becoming either benthic or nektonic (in the case of the midwater ceratioid anglerfishes).

Conservation status

Only one of the anglerfish families, Lophiidae, contains species of economic importance. These are harvested commercially in U.S., European, and Japanese waters, and the species that occurs off the Atlantic Coast of the United States, *L. americanus*, has received protection from the U. S. National Marine Fisheries Service owing to overfishing both for the meat, which is marketed in the United States as monkfish, and the liver, which is highly prized in Japan. The IUCN lists the spotted handfish (*Brachionichthys hirsutus*) of Tasmania as Critically Endangered. The population of this species has been greatly reduced by an introduced starfish that preys on its egg clusters.

Significance to humans

Other than the lophiid species that are harvested commercially, lophiiform fishes have little importance to humans.

A painted frogfish (*Antennarius pictus*) near the Russell Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

1. Male seadevil (*Cryptopsaras couesii*); 2. Sargassumfish (*Histrio histrio*); 3. Big-eye frogfish (*Antennarius radiosus*); 4. Longnose batfish (*Ogcocephalus corniger*); 5. Monkfish (*Lophius americanus*). (Illustration by Joseph E. Trumpey)

Species accounts

Big-eye frogfish
Antennarius radiosus

FAMILY
Antennariidae

TAXONOMY
Antennarius radiosus Garman, 1896.

OTHER COMMON NAMES
English: Singlespot frogfish.

PHYSICAL CHARACTERISTICS
The big-eye frogfish has skin with closely set, forked dermal spinules. The illicium is about as long as the second dorsal fin spine and has no dermal spinules. There is a single dark spot (ocellus) surrounded by a lightly colored ring below the posterior portion of the soft dorsal fin.

DISTRIBUTION
The big-eye frogfish occurs in the western Atlantic Ocean from Long Island, New York, to Florida and across the northern Gulf of Mexico. It has been reported from the eastern Atlantic, but it is apparently very rare there. It has been taken at depths ranging from 20 to 900 ft (6–275 m).

HABITAT
Like other members of its genus, the big-eye frogfish is benthic. This species is primarily an inhabitant of mud bottoms. It is commonly taken by shrimp trawlers in the northern Gulf of Mexico, and it is frequently found in deeper portions of higher-salinity estuaries.

BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Like other frogfishes and most other anglerfishes, the big-eye frogfish is a voracious ambush predator and will take any prey it can capture.

REPRODUCTIVE BIOLOGY
Unknown.

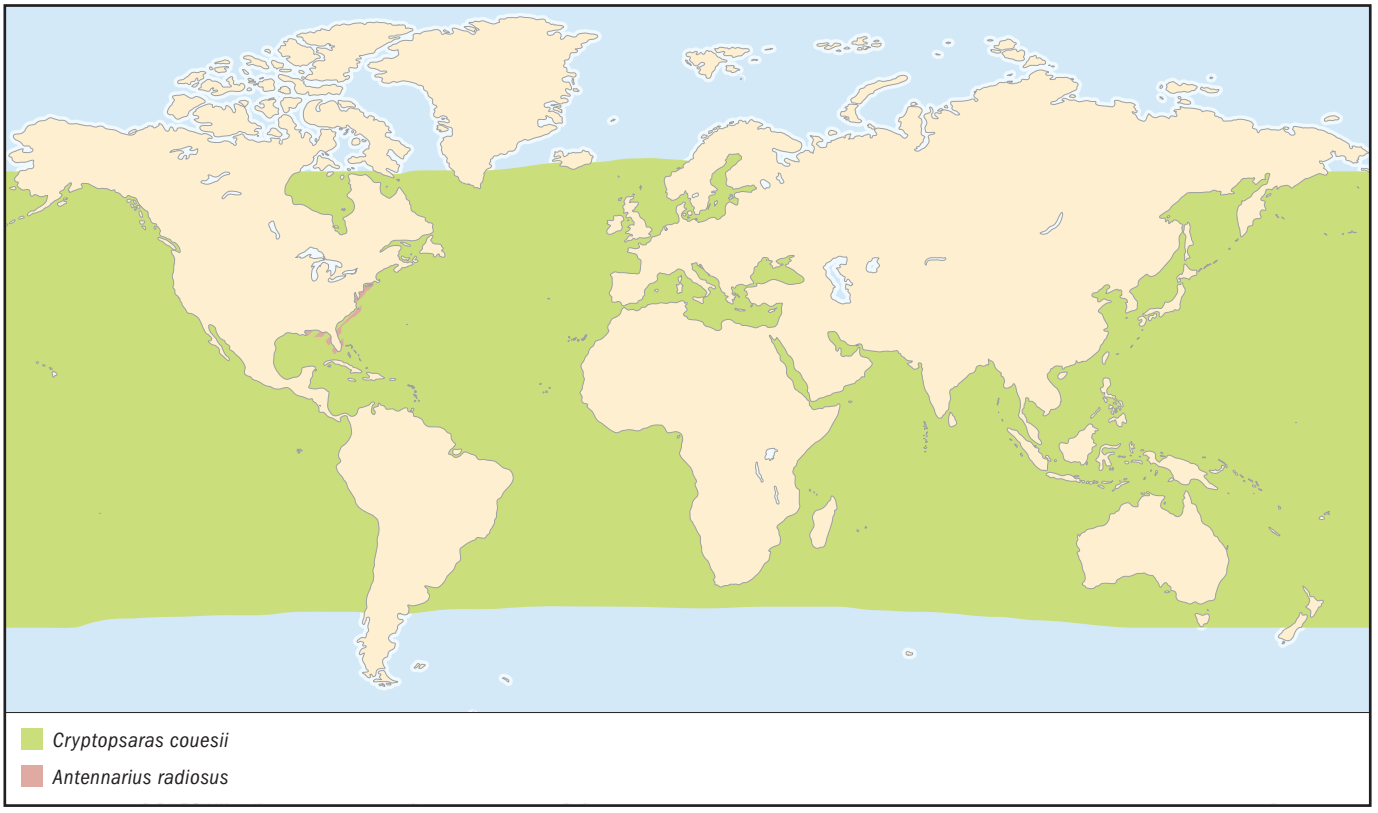
CONSERVATION STATUS
Not threatened. A significant death rate may result from those that are taken as bycatch by shrimp trawlers.

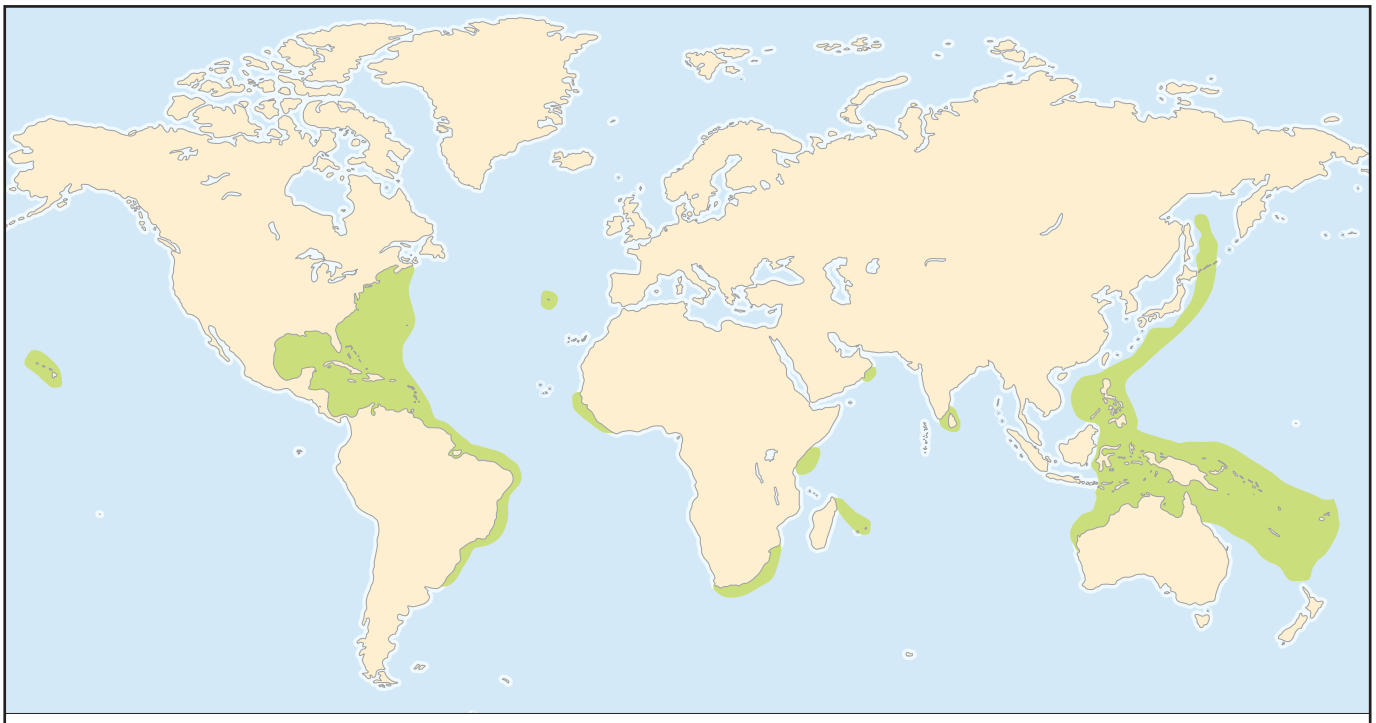
SIGNIFICANCE TO HUMANS
None known. ◆

Sargassumfish
Histrio histrio

FAMILY
Antennariidae

TAXONOMY
Histrio histrio (Linnaeus, 1758).





OTHER COMMON NAMES
English: Sea mouse, mousefish.

PHYSICAL CHARACTERISTICS
Frogfishes (family Antennariidae) are somewhat similar to their monkfish relatives in that they have a large head on which are located several isolated dorsal fin spines; the pectoral fins appear armlike. They are strikingly different in that the head is globose and the body is flattened laterally (compressed) rather than dorsally (depressed). In addition, the second and third dorsal fin spines usually are surrounded by so much fleshy skin that it may be difficult to recognize them as fin spines. The second, or soft, dorsal and anal fins are much more conspicuous, and the soft dorsal is usually much longer than the anal fin. The sargassumfish is characterized by its very short angling apparatus and its smooth skin, which lacks the small, spiny scales or dermal spinules typical of most other frogfishes. Its color pattern is changeable and highly variable, but it is usually cryptic, consisting of streaks, spots, and mottling of brown, olive, and yellow, making it nearly impossible to detect among the sargassum weed in which it hides.

DISTRIBUTION
The sargassumfish has the widest geographic distribution of any frogfish. Being an obligate associate of sargassum weed, they are found wherever this species occurs, that is, in tropical, warm temperate, and occasionally cool temperate waters of the Atlantic, Pacific, and Indian Oceans. They appear to be very rare in the eastern Atlantic, and they are absent from the eastern Pacific.

HABITAT
The sargassumfish is the only frogfish species that is not benthic. It is only found associated with the epipelagic brown algae, *Sargassum*, in tropical and warm temperate environments. Although *Sargassum* is usually pelagic, members of the community associated with it, including the sargassumfish, are technically pseudopelagic.

BEHAVIOR
Most of what is known about the behavior of sargassumfish is associated with their feeding. This behavior is described in the introductory section.

FEEDING ECOLOGY AND DIET
Like most other anglerfishes, sargassumfish are ambush predators that use aggressive mimicry to attract prey. Most observers describe them as particularly voracious, feeding readily and indiscriminately on anything they can swallow, including fishes as long as or longer than themselves. They even consume other sargassumfish. They are one of the major predators of the sargassum community.

REPRODUCTIVE BIOLOGY
Reproduction in the sargassumfish is similar to the known reproductive behavior of other anglerfishes. The eggs are released in the typical egg veil or raft, which in sargassumfish may be 35–47 in (90–120 cm) long and 2–4 in (5–10 cm) wide.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Seadevil
Cryptopsaras couesii

FAMILY
Ceratiidae

TAXONOMY
Cryptosaras couesii Gill, 1883.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Like other midwater anglerfishes, the seadevil is characterized by the absence of pelvic fins, pseudobranchs, and scales or other dermal derivatives. Moderate to extreme degrees of sexual dimorphism characterize members of this suborder. Ceratiids exhibit extreme sexual dimorphism, with the adult males being reduced to ectoparasites of the females. As with most species, the lure (esca) appears to be bioluminescent in the seadevil. Female seadevils have a vertical to strongly oblique mouth, and the first two or three rays of the soft dorsal fin are modified as caruncles (low, fleshy appendages).

DISTRIBUTION
Their distribution is worldwide between 63° N and 43° S latitudes.

HABITAT
The species inhabits the lower mesopelagic and bathypelagic zones, between 246 and 13,123 ft (75–4,000 m), but is most commonly found between 1,640 and 4,101 ft (500–1,250 m).

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Ceratioid anglerfishes, like the seadevil, are one of the most important groups of predatory fishes in the lower mesopelagic and bathypelagic zones of the world oceans. Feeding is by aggressive mimicry using the angling apparatus. They feed upon zooplankton and nekton, with fishes and cephalopods probably forming a major component of the diet.

REPRODUCTIVE BIOLOGY
The reproductive adaptations found among the ceratioid anglerfishes are among the most fascinating in the animal kingdom. As mentioned earlier, all lophiiform anglerfishes appear to have some degree of sexual dimorphism in the structure and size of the olfactory organs. It is assumed that this is associated with the females' production of species-specific pheromones, which attract the males when the female is ready to breed. In ceratioid anglerfishes this sexual dimorphism has reached its extreme, not only among the vertebrates but also perhaps the entire animal kingdom. In most of the 11 ceratioid families, the female is considerably larger than the male (females range from three to 13 times the length of conspecific males). Furthermore, in at least four ceratioid families the males have been so drastically reduced that they have become essentially a pair of swimming testes directed by a huge pair of olfactory organs. Once these "minimized" males find a female, they attach themselves to her with their jaws, eventually achieving histological fusion and leading the remainder of their lives as essentially a pair of "ectoparasitic" testes.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Monkfish
Lophius americanus

FAMILY
Lophiidae

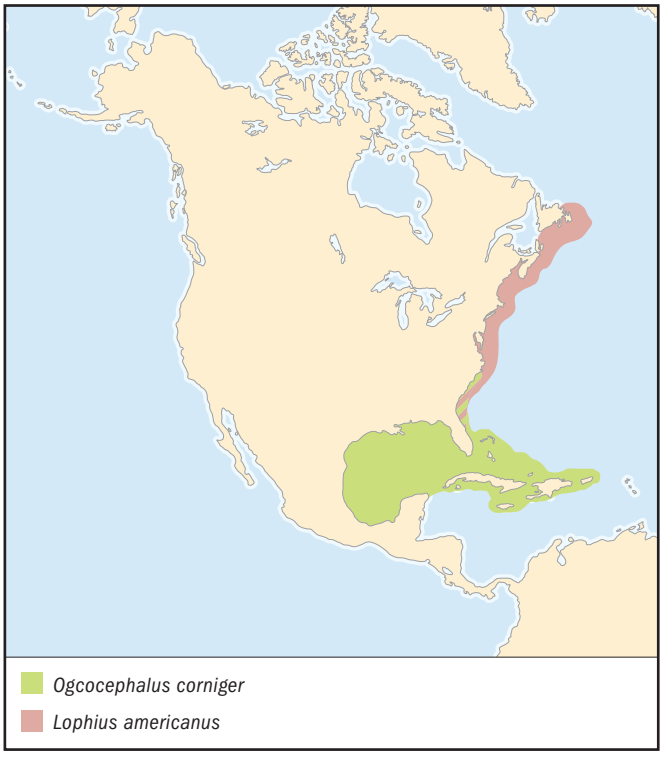
TAXONOMY
Lophius americanus Curvier and Valenciennes in Valenciennes, 1837, North America.

OTHER COMMON NAMES
English: Goosefish, anglerfish.

PHYSICAL CHARACTERISTICS
Like most lophiid anglerfishes, the monkfish is distinguished easily from other anglerfishes by its very large, wide, flattened head. Lophiids also have an enormous mouth armed with long, sharp, conical teeth, and the angling apparatus and second dorsal fin spine arise very close to each other at the anterior end of the snout. The monkfish has a number of derived character states, among which are increased numbers of dorsal and anal fin rays and vertebrae, gill openings restricted to a location completely behind the pectoral fin base, and a variety of cranial osteological features. The monkfish is distinguished from its congeners by several morphological characters.

DISTRIBUTION
The monkfish is known to occur from the Grand Banks off Newfoundland south to the east coast of Florida (about 29° N latitude) and from just below the tide line (only at high latitudes) to depths of more than 2,625 ft (800 m). However, few large individuals are taken below 1,312 ft (400 m). This is the only member of the genus found in the western Atlantic north of Cape Hatteras.

HABITAT
Adult monkfish have been found on soft and hard substrates including soft mud, soft sand, hard sand, pebbles, gravel, and broken shells.



BEHAVIOR
Most of what is known about lophiid behavior comes from observations of the monkfish and another species, *Lophius piscatorius*; general aspects of this behavior are described earlier, in the ordinal account. Aristotle made the very first observations of angling behavior. He described them as having hairlike filaments hung before their eyes, with knobs attached like bait to the end of each filament. When little fishes come in range of the filaments and strike at them, they are led down with the filaments into the monkfish's mouth. Such observations were not recorded again until 1925, when Bigelow and Welsh reported the observations of W. F. Clapp, who observed monkfish catching young tomcod (*Microgadus tomcod*) in the eelgrass beds of Duxbury Bay, Massachusetts.

FEEDING ECOLOGY AND DIET
Like all lophiiform anglerfishes, monkfishes are voracious ambush predators. Their diet consists primarily of fishes, and when given a choice, they prefer soft-rayed fishes to spiny-rayed species. When the opportunity presents itself, however, they take any prey large enough to engulf. This includes fishes nearly as long as itself. The alternate name goosefish alludes to the fact that the monkfish has been known to engulf marine birds when it enters shallow coastal waters at high latitudes during the winter months. (Cormorants, herring gulls, widgeons, scoters, loons, guillemots, razor-billed auks, grebes, and other diving fowl, such as scaup ducks and mergansers, have all been recorded as stomach contents.) Smaller monkfishes are known to feed on a wide variety of invertebrates, including small lobsters, crabs, squid, and polychaetes.

REPRODUCTIVE BIOLOGY
As mentioned earlier, the monkfish is one of the few lophiid species for which detailed life history information is available. Long, mucoid egg veils are characteristic of this species.

CONSERVATION STATUS
During the latter few decades of the twentieth century, the popularity of monkfish increased steadily in U. S. markets. Because the liver also is highly sought by the Japanese market, fishing pressure on this species has resulted in overexploitation. Fortunately, this species has received some protection from the U. S. National Marine Fisheries Service. This species is not listed by the IUCN.

SIGNIFICANCE TO HUMANS
As *Lophius americanus* has gained popularity with consumers in the United States and there is strong demand for it in the Japanese market, this species has tremendous economic importance. ◆

Longnose batfish
Ogcocephalus corniger

FAMILY
Ogcocephalidae

TAXONOMY
Ogocephalus corniger Bradbury, 1980.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Most batfishes are dorsoventrally flattened. They have only a single, very short dorsal fin spine (the illicium), although the vestige of the second spine may be present but embedded. The illicium usually is contained within a deeply concave illicial cavity, and it typically extends forward and downward rather than forward and upward, as in most other anglerfishes. The skin is covered with prominent, tubercle-like scales, which may be very large and conical (bucklers) in some genera. The scales fuse at the anterior end of the snout, forming a moderate to greatly elongated rostrum. The mouth is relatively small compared with other anglerfishes and has small teeth. The longnose batfish has a long, slender rostrum at the end of a triangular head and dark bands of pigment on the distal portions of the pectoral and caudal fins. The overall body color is dark brown or gray, with small, pale spots uniformly distributed on the dorsal surface.

DISTRIBUTION
The longnose batfish inhabits the western Atlantic from Cape Lookout, North Carolina, south to the Yucatan Peninsula, including the Gulf of Mexico and the Caribbean. It has been taken at depths ranging from 95 ft (29 m) to 755 ft (230 m).

HABITAT
All batfishes are benthic, occurring on a wide variety of bottom types.

BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Batfishes feed using aggressive mimicry, as do most anglerfishes; however, they are unusual among anglerfishes in that a greater proportion of their diet seems to be small, benthic invertebrates.

REPRODUCTIVE BIOLOGY
Unknown.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Books

Collette, Bruce B., and Grace Klein-MacPhee, eds. *Bigelow and Schroeder's Fishes of the Gulf of Maine.* 3rd edition. Washington, DC: Smithsonian Institution Press, 2002.

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Pietsch, T. W., and D. B. Grobecker. *Frogfishes of the World: Systematics, Zoogeography, and Behavioral Ecology.* Stanford: Stanford University Press, 1987.

Robins, C. Richard, and G. Carleton Ray. *A Field Guide to Atlantic Coast Fishes: North America.* Boston: Houghton Mifflin Co., 1986.

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Periodicals

Bigelow, H. B., and W. W. Welsh. "Fishes of the Gulf of Maine." *Bulletin of the U. S. Bureau of Fisheries* 40, no. 1 (1925): 1–567.

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———. "The Systematics and Distribution of the Lophiid Anglerfishes. III. Intergeneric Relationships." *Copeia* 1985, no. 4 (1985): 870–875.

Hoffman, H. A., and D. S. Jordan. "A Catalog of the Fishes of Greece, with Notes on the Names Now in Use and Those Employed by Classical Authors." *Proceedings of the Academy of Natural Sciences of Philadelphia* (1892): 230–285.

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John H. Caruso, PhD

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Mugiliformes
(Mullets)

Class Actinopterygii
Order Mugiliformes
Number of families 1

Photo: The white mullet (*Mugil cerema*) is native to the East Coast of the United States, from Massachusetts to Texas. (Photo by Tom McHugh/Shedd Aquarium, Chicago/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

A revision in 1997 recognized 14 genera and 62 species of mullets as valid. Their relationships to other spiny-rayed teleosts are unclear. Skeletal features suggest affinities either to perciforms or to atherinomorphs. Morphological analyses have indicated that mugilids are part of the group Smegmamorpha, with the Synbranchiformes (swamp and spiny eels), Elassomatidae (pygmy sunfishes), Gasterosteiformes (sticklebacks, pipefishes, and relatives), and Atherinomorpha (silversides, livebearers, and relatives). Analyses of complete mitochondrial DNA sequences indicate that mugilids are related most closely to atherinomorphs and that the Synbranchiformes form the next most closely related group to the mugilids and atherinomorphs.

According to anatomical studies of the pharyngobranchial region of the head, *Agonostomus* is the most primitive of the mugilid genera. *Joturus*, *Cestraeus*, and *Aldrichetta* are, respectively, the next most derived lineages. Evolutionary relationships between the remaining, higher mullets, such as *Mugil*, *Myxus*, *Liza*, and *Valamugil* have not been resolved in published work. The oldest known mugilid fossils are skeletal remains of *Mugil princeps*, collected from 30- to 40-million-year-old Menilite beds of Poland and the Ukraine.

Physical characteristics

Most species commonly reach about 7.9 in (20 cm) in total length, but some (e.g., *Mugil cephalus*) may attain 31.5–39.4 in (80–100 cm). The head is broad and flattened dorsally in most species. The snout is short, and the mouth is small. The gill arches of many species are specialized, forming a characteristic pharyngobranchial organ that has an expanded, denticulate pad used for filtration of ingested material. In many (but not all) species of mullets, the teeth are positioned on the lips; this is unlike most species of fishes, in which teeth, if present, are attached directly to the jawbones. In most species of mullets, the teeth are very small or may even be absent.

The eyes may be partially covered by adipose tissue. There are two short, well-separated dorsal fins, the first with four spines and the second with eight to ten segmented rays. The anal fin is short, with two or three spines and seven to twelve segmented rays in adults. The pectoral fins are placed high on the body, and the caudal fin is weakly forked. The lateral line is absent. The scales are moderate to large in size, with one or more longitudinal grooves. There are two or more pyloric caeca associated with the stomach, which also has a thick-walled, muscular gizzard in most species. Mullets usually are grayish green or blue dorsally, and their flanks are silvery, often with dark longitudinal stripes. They are pale or yellowish ventrally.

Distribution

Worldwide through tropical, subtropical, and warm temperate regions; some species inhabit cool temperate waters. Several species and genera are common in the Indo-Pacific (e.g., *Liza* and *Valamugil*). *Mugil* generally is restricted to the Atlantic and eastern Pacific.

Habitat

Most mullets are found in coastal marine and brackish waters. They are nektonic, usually in shallow inshore environments, such as coastal bays, reef flats, tide pools, and around harbor pilings and in brackish water estuaries, lagoons, and

Mullets (*Mugil* sp.) in the Homosassa River, Florida, USA. (Photo by Douglas Faulkner/Photo Researchers, Inc. Reproduced by permission.)

mangroves. They usually swim over sandy-muddy bottoms and sea grass meadows, in relatively still waters. They commonly occur at water depths of 65.6 ft (20 m) but may be found offshore or in deeper waters. Many species are euryhaline and move between marine and freshwater environments of rivers and flooded rice fields. Some species occasionally swim far upriver, and a few species spend their entire adult lives in rivers.

Behavior

Feeding behavior apparently follows daily cycles, which may change through the seasons according to water temperature and prey availability. Several species form schools, particularly at night; schooling adults may show leaping behavior, especially during the evening.

Feeding ecology and diet

Mullet fry are planktivorous; larger specimens browse on submerged surfaces and use their pharyngobranchial organ to filter particulate material, microalgae, microorganisms, and small invertebrates, such as polychaetes, crustaceans, and mollusks. Mullets are subject to predation from larger fishes (e.g., drums and basses), crocodiles, birds (in particular, pelicans), and various aquatic mammals such as seals, sea lions, and dolphins. They are also hunted by humans.

Reproductive biology

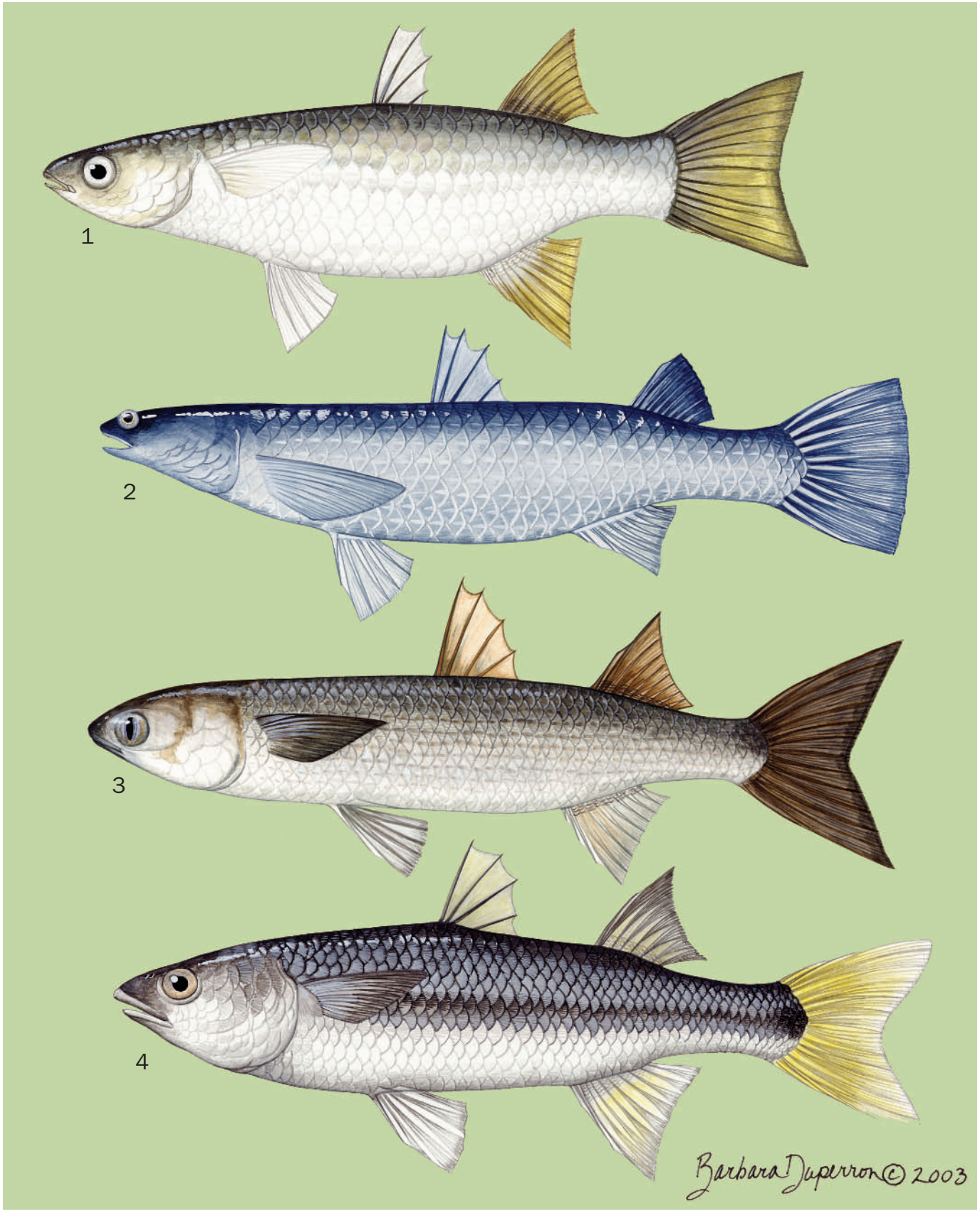
Coastal species typically spawn in shallow open areas or offshore, forming large schools before moving out to the spawning grounds. Freshwater species possibly move downstream to spawn in brackish waters; alternatively they might spawn upstream, and the fry are swept downstream for a short period before subsequently migrating back upriver.

Conservation status

One nominal species, *Liza luciae*, known only from the Saint Lucia estuary, Natal, is considered Endangered according to the 2002 IUCN Red List. A taxonomic revision in 1997 included *Liza luciae* as conspecific with the more widespread *Liza melinoptera*.

Significance to humans

Mullets are important food fishes, caught in subsistence and commercial fisheries, and are used in aquaculture in many parts of the world. Food and Agriculture Organization (FAO) statistics give the global commercial capture of mullets for 2000 as 409,892 metric tons (26% from China). Global aquaculture of mullets in 2000 was 100,091 metric tons (80% coming from Egypt), with a value of almost $333.4 million dollars.



1. Large-scale mullet (*Liza grandisquamis*); 2. Shark mullet (*Rhinomugil nasutus*); 3. Flathead mullet (*Mugil cephalus*); 4. Mountain mullet (*Agonostomus monticola*). (Illustration by Barbara Duperron)

Species accounts

Mountain mullet
Agonostomus monticola

FAMILY
Mugilidae

TAXONOMY
Mugil monticola Bancroft, 1834, Jamaica. *Agonostomus monticola* is morphologically variable. Several different species have been recognized from Central America and the West Indies, but a review in 1997 listed them as conspecific.

OTHER COMMON NAMES
French: Mulet de fleuve; Spanish: Lisa de río, tepemechín.

PHYSICAL CHARACTERISTICS
Grows to 14.2 in (36 cm) in total length. Dorsal surface of head is convex between the eyes. Teeth are small and attached directly to the jawbones. Pharyngobranchial organ is rudimentary. There are 16–23 gill rakers on the lower part of first gill arch. Anal fin has two spines and 10 soft rays in adults. There are 38–46 scales in a longitudinal series along the flanks. Body is brownish, sometimes with a silvery band on the flanks from the pectoral to the caudal fin. Dorsal, anal, and caudal fins are dusky yellowish; there is a dark spot at the base of the caudal fin.

DISTRIBUTION
Rivers of the West Indies, Central America, Colombia, Venezuela, and the Galapagos Islands. Occasionally reported from the rivers of Florida and Louisiana.

HABITAT
Freshwaters of fast-flowing hill streams.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Diet varies seasonally. Omnivorous, feeding mainly on insects, prawns, fruits, and algae.

REPRODUCTIVE BIOLOGY
Adults may spawn in the lower reaches of rivers or in the sea. Spawning apparently correlates with peak rainfall. Larvae and juvenile fish spend perhaps six weeks at sea before migrating back upstream.

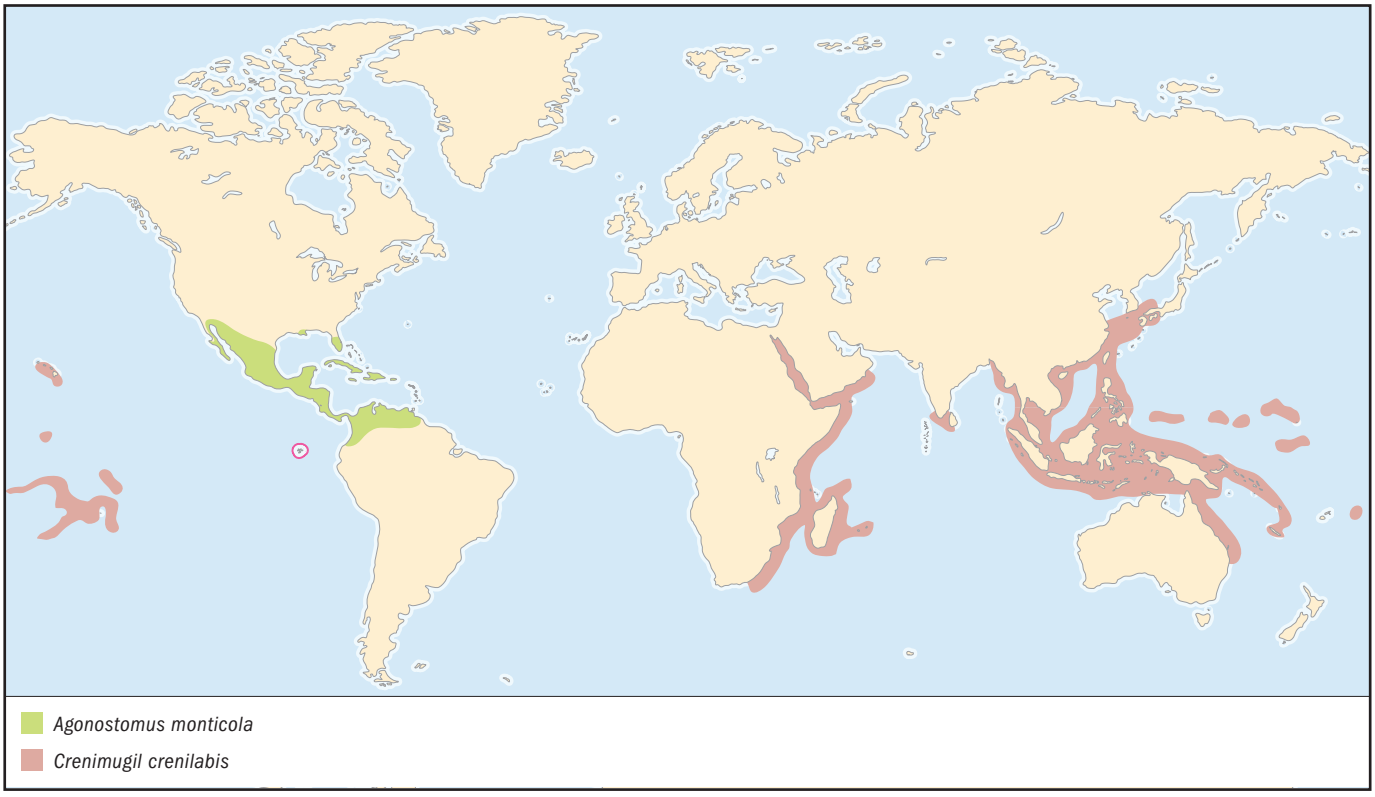
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
There are small commercial and subsistence fisheries in the West Indies and Central America. ◆

Fringelip mullet
Crenimugil crenilabis

FAMILY
Mugilidae

TAXONOMY
Mugil crenilabis Forsskal, 1775, Red Sea.



OTHER COMMON NAMES
French: Mulet boxeur; Spanish: Lisa labride.

PHYSICAL CHARACTERISTICS
Commonly reaches 10.2 in (26 cm) in standard length but may reach 19.7 in (50 cm). The upper lip is very thick, with up to 10 rows of small papillae in fish larger than 2.4 in (6 cm). There are no teeth on the lips. The anal fin has three spines and usually nine soft rays in adults. There are 36–42 scales in a longitudinal series along the flanks. Body is olive-green dorsally and silvery on the flanks and abdomen. Pectoral fins are yellowish, with a distinct dark purplish spot at the upper part of the fin base.

DISTRIBUTION
Indo-Pacific, from the Red Sea to Polynesia.

HABITAT
In shallow waters (up to 65.6 ft, or 20 m) of lagoons with sandy and muddy bottoms, reef flats, tide pools, and harbors.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Larvae and juveniles probably feed on plankton. Adults probably feed on particulate organic material, algae, and invertebrates.

REPRODUCTIVE BIOLOGY
Adult fish form schools in shallow waters around lagoons before spawning.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Small commercial and subsistence fisheries, particularly in Polynesia; some aquaculture. ◆

Large-scale mullet
Liza grandisquamis

FAMILY
Mugilidae

TAXONOMY
Mugil grandisquamis Valenciennes, 1836, Gorée, Senegal.

OTHER COMMON NAMES
French: Mulet écailleux; Spanish: Liza escamuda.

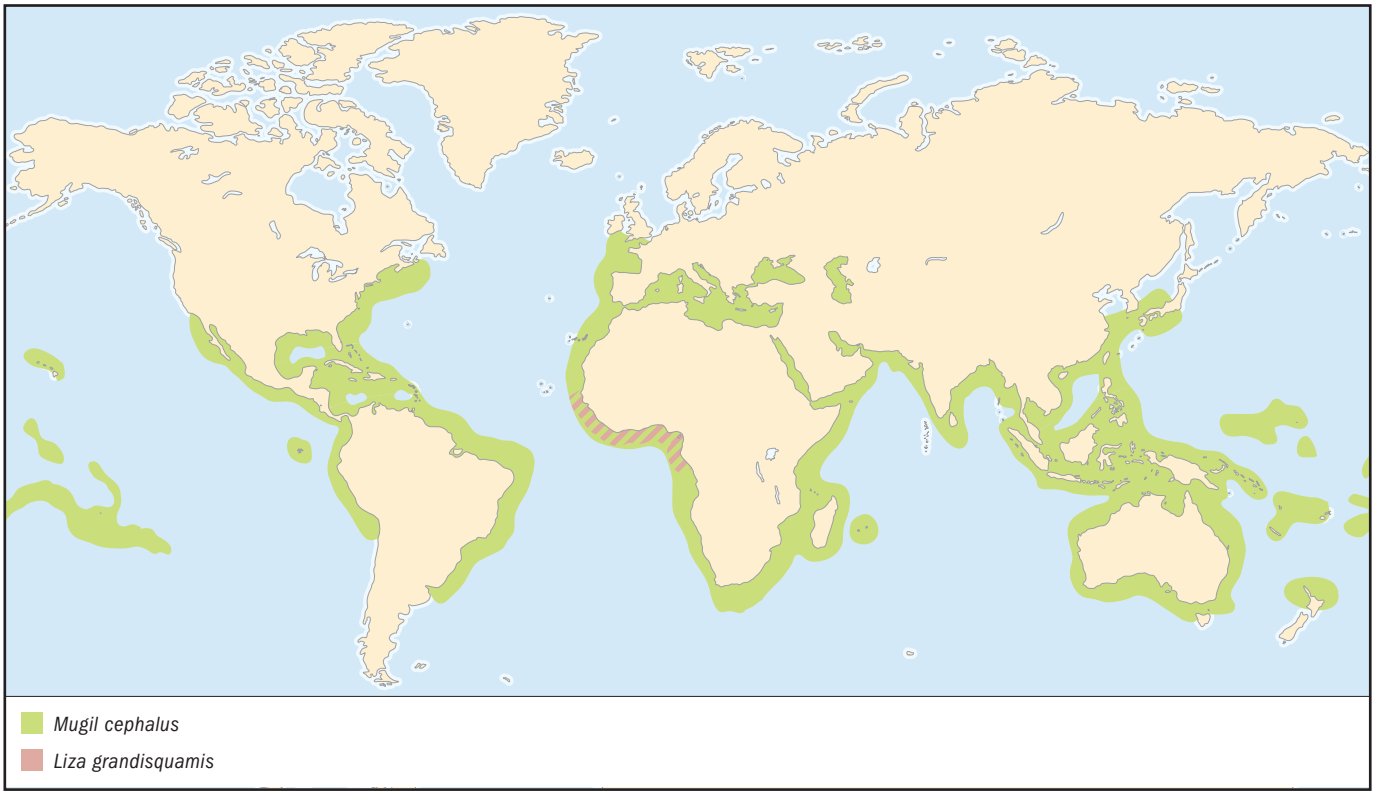
PHYSICAL CHARACTERISTICS
Commonly reaches 9.8 in (25 cm) in standard length but may reach up to 15.7 in (40 cm) in fork length. Teeth on both lips are absent or are very small, well spaced, and positioned in a single row on the upper lip, or rarely, in two rows. The anal fin has three spines and nine soft rays in adults. There are 26–30 scales in a longitudinal series along the flanks. Body is darkish dorsally and slightly paler and silvery laterally and ventrally. The anal fin and lower lobe of the caudal fin may be yellowish.

DISTRIBUTION
West Africa from Senegal to the Republic of Congo.

HABITAT
Usually found in brackish waters covering muddy substrates, such as mangroves, creeks, estuaries, and inundated mudflats.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Adults feed in schools, mostly at night, on particulate organic matter, mud, diatoms, algae, microarthropods, foraminiferans,



and free-living nematodes. During the wet season fish take a greater proportion of fine organic material than coarser sands, because increased rainfall brings more fine allochthonous material into rivers and "washes" the sand sediments free of fine food material.

REPRODUCTIVE BIOLOGY
Populations from the Ebrie lagoon, Ivory Coast, do not show a seasonal spawning cycle; spawning occurs principally in the lagoon but also may occur in the sea.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Small commercial and subsistence fisheries. A potentially important species for aquaculture. ◆

Flathead mullet
Mugil cephalus

FAMILY
Mugilidae

TAXONOMY
Mugil cephalus Linnaeus, 1758, European seas. It has been suggested that several species, initially distinguished by slight differences in morphological features, fin ray counts, dentition, and fin coloration, are synonymous with *Mugil cephalus.* Some authors have indicated that the concept of *Mugil cephalus* as a widespread, polymorphic species may be incorrect. According to comparative analyses of the morphometrics, isozymes, and mitochondrial DNA of populations of *Mugil cephalus* from around the world, however, the variation between populations is not large enough to indicate definitively that they are differentiated species.

OTHER COMMON NAMES
English: Striped mullet, black mullet; French: Mulet cabot; Spanish: Lisa pardete.

PHYSICAL CHARACTERISTICS
Commonly reaches 13.8 in (35 cm) in total length but may reach 47.2 in (120 cm) in standard length. Adipose tissue covers most of the eye. There are several rows of very small unicuspid and bicuspid teeth on the edges of the lips. Anal fin has three spines and eight soft rays in adults. There are 36–44 scales in a longitudinal series along the flanks. Body is olive-green dorsally and silvery on the flanks and abdomen, with about seven longitudinal dark stripes along the flanks. The pelvic fin, anal fin, and lower lobe of the caudal fin are yellowish in some populations.

DISTRIBUTION
Worldwide in tropical, subtropical, and warm temperate waters from 42° S latitude to almost 51° N latitude; less abundant in the tropics.

HABITAT
Tolerant of salinity levels from zero to 81 parts per thousand (freshwater to hypersaline) and temperatures from 41°F (5°C) to 98.6°F (37°C). Inhabits inshore marine waters, estuaries, lagoons, and rivers, usually in shallow waters, and rarely moving deeper than 656 ft (200 m). Adults may move far upriver.

BEHAVIOR
The adults form schools and sometimes jump.

FEEDING ECOLOGY AND DIET
Larvae and juveniles feed on plankton. Adults feed on particulate organic material, algae, and invertebrates. Fish may gulp and filter sediment, browse over submerged surfaces, or feed at the surface.

REPRODUCTIVE BIOLOGY
Adult fish move offshore in shoals to spawn, usually at night, before returning to inshore brackish waters and freshwaters. Fry and juveniles remain in sheltered bays, lagoons, and estuaries until they are sexually mature.

CONSERVATION STATUS
Not threatened.

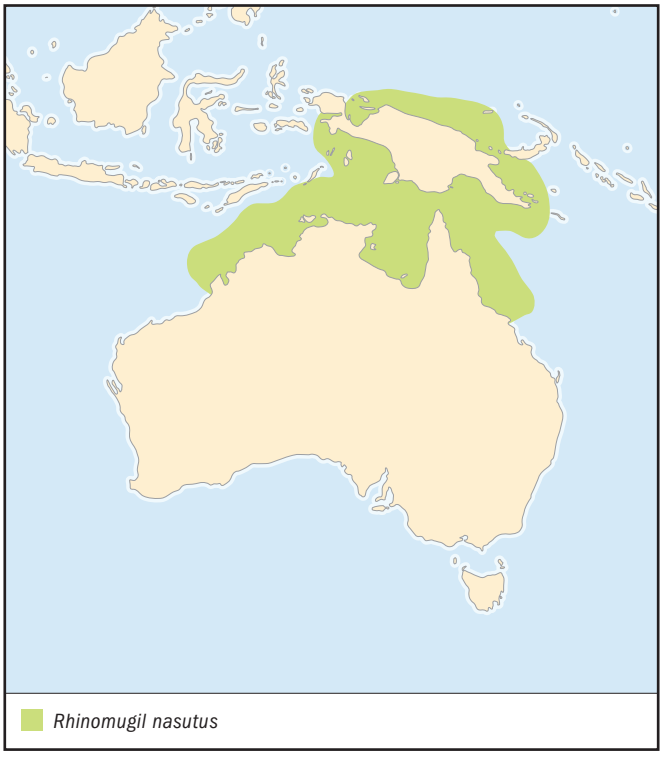
SIGNIFICANCE TO HUMANS
Major commerical and subsistence fisheries in many parts of the world. Food and Agriculture Organization (FAO) of the United Nations statistics give the global commercial capture of flathead mullets for 2000 as 29,335 metric tons (18% and 19% coming from Mexico and Venezuela, respectively). Global aquaculture of flathead mullets in 2000 was 89,078 metric tons (90% coming from Egypt), with a value of almost $312.3 million dollars. ◆

Shark mullet
Rhinomugil nasutus

FAMILY
Mugilidae

TAXONOMY
Mugil nasutus De Vis, 1883, Cardwell, Rockingham Bay, Queensland, Australia.

OTHER COMMON NAMES
English: Mud mullet.



PHYSICAL CHARACTERISTICS
Reaches 12.6 in (32 cm) in fork length. The shark mullet looks unlike other mullets, because the eyes are positioned high, toward the top of the head, which is concave between the eyes. Nostrils are placed low on the snout, which projects beyond the upper lip. Teeth on both lips are small and spatulate. The anal fin has three spines and eight soft rays in adults. There are 28–30 scales in a longitudinal series along flanks. Body is slate gray dorsally and silvery laterally and ventrally; the fins are yellowish.

DISTRIBUTION
Tropical Australia and New Guinea.

HABITAT
Usually occurs in muddy freshwaters and coastal water habitats, such as mangroves.

BEHAVIOR
Swims in schools at the water surface, with the eyes and snout exposed. Apparently capable of breathing air and wriggling for short distances over mud banks.

FEEDING ECOLOGY AND DIET
Feeds on muddy substrates and may feed on algae and insects at the water surface.

REPRODUCTIVE BIOLOGY
Little is known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No reported fisheries data. Species of *Rhinomugil* (usually *Rhinomugil corsula*) are sold in the aquarium trade, because of their similarity to species of four-eyed fish (*Anableps*). ◆

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Ian J. Harrison, PhD

Atheriniformes

(Rainbowfishes and silversides)

Class Actinopterygii
Order Atheriniformes
Number of families 8

Photo: A salmon rainbowfish (*Glossolepis incisus*). (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Atheriniformes originally was conceived by Donn Rosen in 1964 to include the exocoetoids (flying fishes and allies), scomberesocoids (sauries), adrianichthyoids (ricefishes), cyprinodontoids (killifishes and allies), atherinoids (silversides and allies), and phallostethoids (priapium fishes). Today this disparate assemblage of fishes still is thought to be a natural group, but it has been parceled into three orders. Now called the Atherinomorpha, the group contains the orders Cyprinodontiformes and Beloniformes (put together as Division II atherinomorphs by Rosen and Parenti in 1981) and the Atheriniformes (Division I atherinomorphs according to Rosen and Parenti). Characters of the testis, egg, embryo, rostral cartilage and skull, and dorsal gill arch skeleton, among others, unite the Atherinomorpha. This chapter concerns the Atheriniformes, which at present includes the silversides, phallostethids, rainbowfishes, and related taxa.

At more than 50 million years old, fossils of the genus *Atherinidarum* from the early Eocene of France are the oldest known atheriniforms. Researchers disagree about the identity of the most basal atheriniform lineages and have variously proposed both freshwater (bedotiids and melanotaeniids) and partly or wholly marine (atherinopsids and notocheirids) groups. Through the course of their evolution different groups of atheriniforms have repeatedly breached the marine-freshwater barrier. Such an ability to colonize patchily distributed freshwater habitats has fostered speciation within the order, especially in the Americas and Australia. At present there are about 315 species and 49 genera of atheriniforms known to science.

Ichthyologists disagree on whether the Atheriniformes are a monophyletic group, descended from a single branch on the atherinomorph tree, or a hodgepodge of lineages on multiple branches that are associated closely with the Cyprinodontiformes and Beloniformes (which are considered sister groups). Even the number and constitution of families is in dispute: recent classifications have cited from six to ten families. In light of the disagreement in the literature, this treatment follows Joseph Nelson's book *Fishes of the World*, in which eight families are recognized within the order: Bedotiidae (Malagasy rainbowfishes), Melanotaeniidae (rainbowfishes), Pseudomugilidae (blue-eyes), Telmatherinidae (Sulawesi rainbows), Atherinidae (silversides), Notocheiridae (surf silversides), Dentatherinidae (pygmy or tusked silverside), and Phallostethidae (priapium fishes).

In 1996, the most recent treatment of the issue, Dyer and Chernoff marshaled 10 morphological characters supporting the Atheriniformes as a monophyletic, or natural, group. In addition, they proposed a new classification for the order, in which the number of families was reduced to six. Familial allocations within this new classification are in stark contrast to Nelson's scheme. Differences include an expansion of the family Melanotaeniidae to subsume the families Bedotiidae, Pseudomugilidae, and Telmatherinidae; an expansion of the family Phallostethidae to include Dentatherinidae; and an elevation of the Old World silverside genus *Atherion* to family status (Atherionidae). Furthermore, in agreement with a 1994 article by Saeed and collaborators, the New World silverside subfamilies Menidiinae and Atherinopsinae are shunted from the family Atherinidae into their own family, Atherinopsidae. Dyer and Chernoff's morphology-based hypothesis awaits further testing, especially using DNA sequence data. It is too soon to say whether their proposal will gain wide acceptance. Certainly, though, theirs will not be the last word on atheriniform relationships.

A school of silversides (Atherinidae), near Thailand. (Photo by Animals Animals ©Joyce & Frank Burek. Reproduced by permission.)

Physical characteristics

A reasonable degree of morphological diversity is found among the Atheriniformes, and, in particular, phallostethids exhibit a form that is unique among all fishes. The typical silverside generally is elongate and laterally compressed, with two dorsal fins, a single anal fin spine, usually cycloid scales, and no lateral line. Most are silvery in color and have a prominent mid-lateral stripe along each side of the body. Melanotaeniids are constructed similarly but often are deeper bodied and have sexually dimorphic color patterns. Male rainbowfishes frequently are brilliantly colored, with complex patterns, in various shades of red, yellow, orange, blue, and green. In telmatherinids, as well as some pseudomugilids and melanotaeniids, the anal and dorsal fins sometimes are elongated into filamentous extensions or elaborate fanlike shapes.

Most noteworthy among atheriniforms, however, are the extraordinarily modified phallostethids (priapium fishes). In both male and female phallostethids, the anal and genital openings are shifted anteriorly and are located under the throat. Males have an elaborate, bilaterally asymmetric copulatory structure under the head, called a priapium, for which no parallel exists among other fishes. A suspensory component of the priapium is made up of modified anterior pleural ribs and pelvic bones. Emerging from the posterior end of the priapium and arching forward almost the entire length of the head are the ctenactinia—elongate, curved bones used for clasping the female during mating. In different species, the anus is offset to one or the other side of the priapium, and the seminal papilla is offset opposite the anus. Both open anteriorly. The seminal papilla, which is elaborated into a copulatory organ in some species, is used to transfer bundles of sperm to the female.

Distribution

The Atheriniformes are distributed in mainly coastal areas of tropical and temperate seas throughout the world and also occur in freshwater lakes and streams in many regions. Largely or entirely marine atheriniform families include the Atherinidae, Notocheiridae, and Dentatherinidae. Atherinids occur worldwide in near-shore marine environments and in freshwaters of primarily the Americas and Australia. Members of the atherinid subfamily Menidiinae show a propensity for invasion of freshwater habitats from coastal marine environments. In the lakes and streams of the Mesa Central of southern Mexico, freshwater menidiines have diversified into a species flock of 20 or so closely related species with exceedingly circumscribed ranges (many are found in only a single lake). Notocheirids are exclusively marine: five species of the genus *Iso* are distributed along the coasts of South Africa, India, Japan, Australia, and Hawaii, and the species *Notocheirus hubbsi* is found only along the coast of Chile. Finally, the family Dentatherinidae consists of but a single species, *Dentatherina merceri*, from the inshore seas of the Philippines, New Guinea, and northeastern Australia.

All of the remaining atheriniform families are predominantly freshwater and are wholly restricted to Australia and the Indo-Pacific region, except for the Bedotiidae from the freshwaters of Madagascar. Rainbowfishes of the family Melanotaeniidae are abundant in New Guinea at elevations below 5,249 ft (1,600 m) as well as on numerous islands to the west of New Guinea. Additionally, they are found in Australia, mostly in river drainages in the northern and eastern regions of the continent. Pseudomugilids, from New Guinea, Australia, and Indonesia, and telmatherinids, from Sulawesi and Indonesia, can be found in fresh, brackish, and marine waters. Likewise, phallostethids occur in freshwaters and estuaries of the Southeast Asian mainland, the Philippines, and Sulawesi.

Habitat

Atheriniform habitats are as diverse as the fishes themselves. From the crashing surf zone of a Pacific island, where one might observe the silvery flashes of a school of *Iso*, to the still depths of a rainforest pool in New Guinea, where shoaling rainbowfishes dominate, atheriniforms have adapted to a range of aquatic conditions. Marine silversides can be found in almost all nonpolar, shallow marine habitats, including reefs, estuaries, and lagoons, and in the surf along beaches. Only a few species live in the open water. Freshwater atherini-

Boeseman's rainbowfish (*Melanotaenia boesemani*) are found in New Guinea. Photo by Animals Animals ©M. Gibbs, OSF. Reproduced by permission.)

forms occur in a variety of temperate and tropical lakes and streams, including spring-fed desert waterholes in Australia and mountain lakes in Patagonia.

Behavior

Atheriniforms are gregarious fishes that form schools of various sizes. Some marine silversides aggregate into enormous schools—numbering in the thousands—which cruise just below the surface, continually feeding on plankton. For instance, *Atherinomorus capricornensis* has been observed forming schools more than 328 ft (100 m) long and 65.6 ft (20 m) wide. At night silversides are attracted to bright lights and are caught easily by fishermen for use as bait. Some of the most interesting types of behavior found in atheriniforms, however, relate to reproduction.

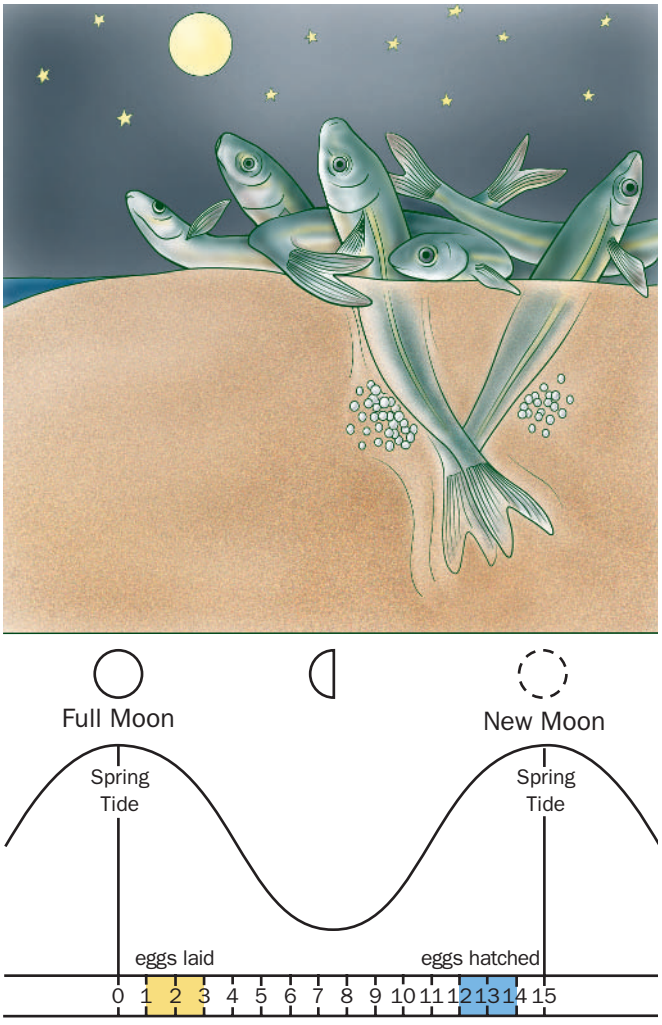
Feeding ecology and diet

In general, atheriniforms are omnivorous, sometimes feeding on algae but depending more heavily on the most abundant forms of invertebrate protein in their respective habitats. For marine species, this means a heavy reliance on minute crustaceans and other forms of zooplankton. Fish larvae also are eaten by some species. In freshwaters, terrestrial insects often represent a significant portion of the diet. This is certainly true for the melanotaeniid rainbowfishes, which have a special preference for ants. In addition, freshwater atheriniforms feed on aquatic insects, zooplankton, and algae. Atheriniforms themselves are preyed upon by birds, mammals, and larger fishes, among other organisms. Marine silversides, in particular, which often aggregate in large schools, are sought after by larger fishes of commercial importance.

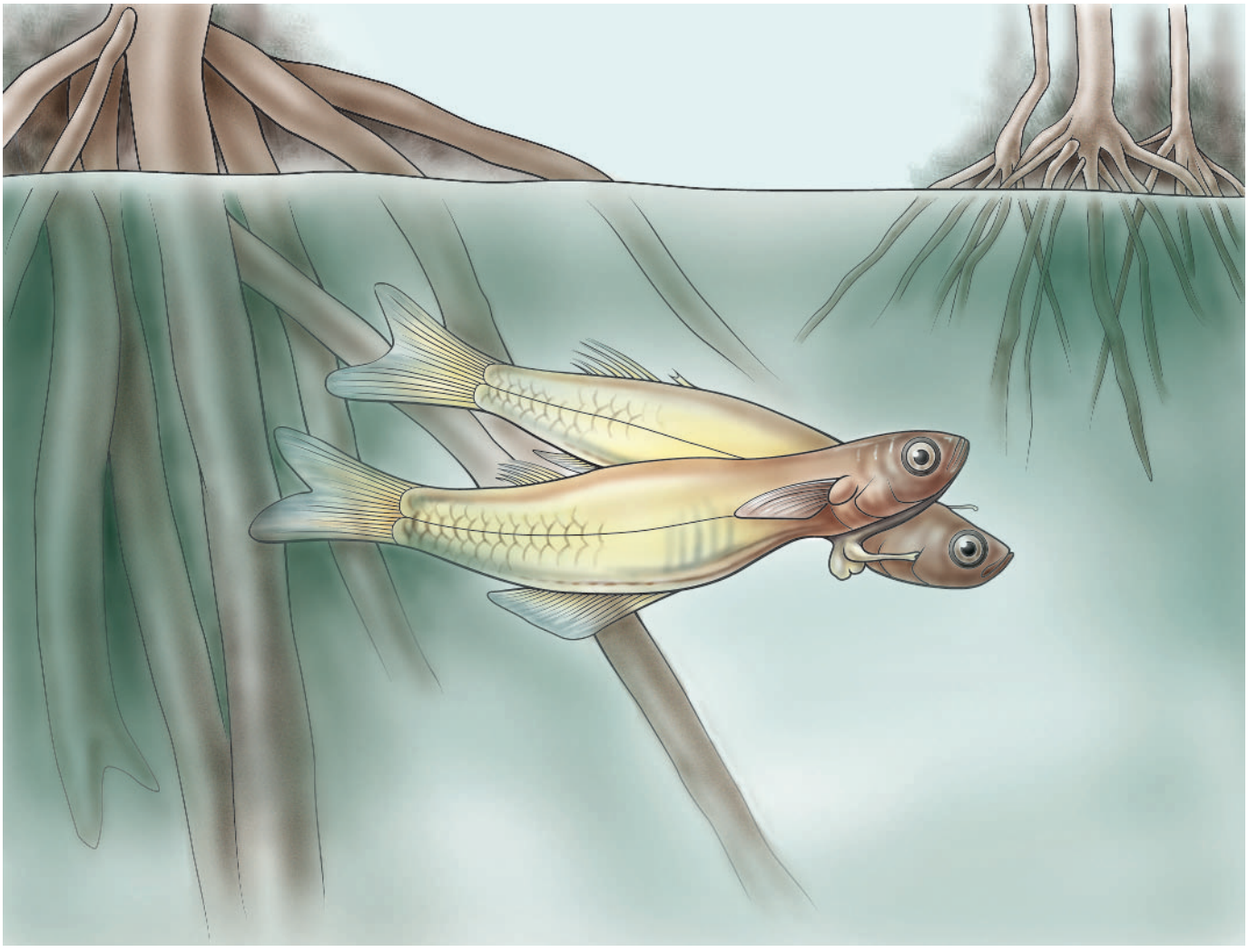
Reproductive biology

Peculiar reproductive repertoires are numerous within the atheriniformes. Large eggs with adhesive filaments are characteristic of the group; the filaments are used to anchor the eggs to aquatic plants or other forms of substrate. Among the rainbowfishes, spawning occurs day after day for an extended period, each day of which the female attaches a small number of thread-bearing eggs, fertilized externally by the male, to underwater plants. Eggs typically hatch in seven to 18 days. Atheriniform larvae generally are large (0.16–0.35 in; 4–9 mm) at hatching, and although they still possess a yolk sac, they have open mouths and can begin feeding immediately.

A truly exceptional reproductive strategy has evolved in grunion (two species of atherinids). *Leuresthes tenuis* and *L. sardina* both time their spawning to take advantage of tidal effects. Grunion spawn during periods of only a few hours on only six nights a month, when tides are highest around the times of the full and new moons (semilunar tides). The fishes ride in with large waves and are left stranded on the sand as the water recedes. Once on the beach, the female burrows into the sand with her tail to lay the eggs, and an accompanying male deposits his milt simultaneously. The fertilized eggs are left buried in the sand a few inches below the surface; they hatch in about two weeks, when semilunar high tides return to uncover them. Possible advantages for the eggs are decreased predation and increased oxygen levels and incubation temperature.



Grunion emerge from the surf to spawn on the beach, laying their eggs soon after the full moon. (Illustration by Patricia Ferrer)



Phallostethids mating; male restrains female with anteriorly situated priapium—a mating organ. (Illustration by Patricia Ferrer)

Male phallostethids, with their bizarre gripping structures (described earlier), ram females, and the two become locked together physically by the priapium during copulation. Frantic bursts of swimming are required for the pair to disengage. Further description of this behavior is provided in the species account of *Neostethis bicornis*.

In a lineage of *Menidia*, sexual reproduction has been forgone entirely. The *Menidia clarkhubbsi* species complex from the Gulf of Mexico is made up of unisexual clonal lineages thought to be the result of hybridization events between *M. beryllina* and an as yet undetermined species, similar to *M. peninsulae*. The unisexuals produce eggs with a complete chromosomal complement that do not require fertilization but must still rely on sperm supplied by one of the bisexual species to stimulate embryo formation. Spawning itself is simple in *Menidia*. A single female—attended by several males—deposits eggs in aquatic vegetation, and the males leave milt; no courtship has been observed.

Conservation status

While no atheriniforms are listed by CITES, 79 species presently are included on the IUCN Red List. Of those, 28 species are listed as Data Deficient, 8 species are listed as Lower Risk/Near Threatened, and 31 species (most of which are rainbowfishes) are listed as Vulnerable. Five species are Endangered: *Poblana letholepis* and *Poblana squamata* from Mexico, *Craterocephalus fluviatilis* and *Pseudomugil mellis* from Australia, and *Melanotaenia boesemani* from New Guinea. Six species are considered Critically Endangered: *Chilatherina sentaniensis* from Irian Jaya, *Glossolepis wanamensis* and *Kiunga ballochi* from Papua New Guinea, *Poblana alchichica* from Mexico, *Rheocles wrightae* from Madagascar, and *Scaturiginichthys vermeilipinnis* from Australia. A single atheriniform, *Rheocles sikorae* from Madagascar, is believed to be Extinct.

A common trend holds true for the threatened atheriniforms: they are restricted to circumscribed freshwater habitats. Such habitats are particularly vulnerable. Water quality often is threatened by pollutants, including nutrients, which

are the byproducts of such human activities as deforestation, mining, and waste disposal. Introduced fish species pose another serious problem; they can be detrimental to native fish populations both as resource competitors and as predators. In the United States—where freshwater atheriniforms are few—there are no atheriniforms listed as Endangered by the U. S. Fish and Wildlife Service. Only one species, *Menidia extensa* (the waccamaw silverside) from North Carolina, is listed as Threatened.

Significance to humans

Because of their small size, most atheriniforms are not sought as sources of food for humans, though there are exceptions to this rule. For instance, some large piscivorous *Odontesthes* species support thriving fisheries in lakes and reservoirs in Peru, Argentina, Chile, and southern Brazil. Marine silversides are indirectly important to commercial fisheries, in that they are an significant food source for many larger fish species that are valued as food fishes. When they are directly fished, small silversides typically are used as bait or converted into pet food.

In contrast, the freshwater rainbowfishes, owing to their extraordinary diversity of colors, are valued highly in the aquarium trade. At present, most of the rainbowfishes sold in pet stores are captive bred, but in the recent past some species were fished heavily to satisfy the demands of mostly European and American aquarists. Indeed, consider the case of the Boeseman's rainbow (see species account), which is considered Endangered. During the 1980s, when the fishery was unrestricted, tens of thousands of individuals were being removed from the wild each month for export.

1. Celebes rainbowfish (*Marosatherina ladigesi*); 2. Boeseman's rainbowfish (*Melanotaenia boesemani*); 3. *Rheocles derhami*; 4. Eendracht land silverside (*Atherinomorus endrachtensis*); 5. Flower of the wave (*Iso rhothophilus*); 6. *Neostethus bicornis*; 7. Inland silverside (*Menidia beryllina*); 8. California grunion (*Leuresthes tenuis*). (Illustration by Patricia Ferrer and Michelle Meneghini)

Species accounts

Eendracht land silverside
Atherinomorus endrachtensis

FAMILY
Atherinidae

TAXONOMY
Atherina endrachtensis Quoy and Gaimard, 1825, Shark Bay, Western Australia. Type locality probably is given in error; more likely, it is New Guinea or Waigeo Island.

OTHER COMMON NAMES
English: Endracht hardyhead, striped hardyhead, striped silverside; Misima-Paneati: Galgal.

PHYSICAL CHARACTERISTICS
Maximum length about 3.3 in (8.5 cm). Elongate, with typical silverside shape. Moderately deep body. Large eyes and silvery midlateral band. Swim bladder visible through translucent flesh.

DISTRIBUTION
Northern Australian coast, Vanuatu, Papua New Guinea, Admiralty Islands, New Britain, Solomon Islands, New Caledonia.

HABITAT
Found in shallow coastal waters.

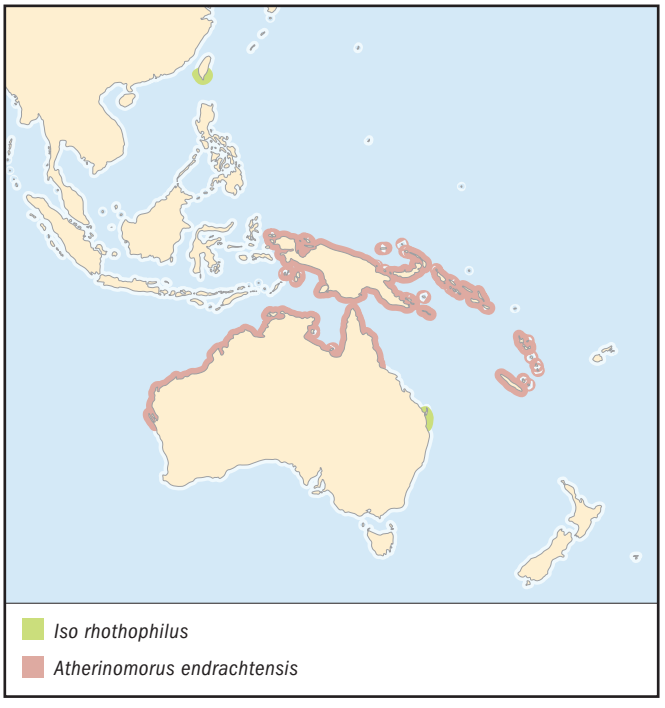
BEHAVIOR
Often schools with other silverside species.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton.

REPRODUCTIVE BIOLOGY
Spawning behavior unknown.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆



California grunion
Leuresthes tenuis

FAMILY
Atherinidae

TAXONOMY
Atherinopsis tenuis Ayres, 1860, San Francisco, California, United States.

OTHER COMMON NAMES
French: Capucette californienne; Spanish: Pejerrey californiano.

PHYSICAL CHARACTERISTICS
Grows to 7.5 in (19.0 cm) maximum length. An elongate silverside with a prominent silvery lateral band and bluish green coloration on the back.

DISTRIBUTION
Monterey Bay, California, to the southern Baja Peninsula.

HABITAT
Coastal marine waters.

BEHAVIOR
Known for its peculiar spawning behavior. When grunion emerge from the surf to spawn on beaches, they can be collected by hand.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton.

REPRODUCTIVE BIOLOGY
Spawns en masse above the waterline on beaches during highest tides of the spring and summer months. Both males and females ride in with large waves and are left exposed on the sand when the water recedes. Females burrow tail first into the sand to deposit their eggs, and attending males fertilize the eggs as they are released. After spawning, adults return to the sea. They are capable of spawning numerous times. The eggs hatch in about two weeks, upon being agitated by another high tide. Buried grunion eggs provide food for shore birds, crabs, isopods, and beetles.

CONSERVATION STATUS
Not threatened.

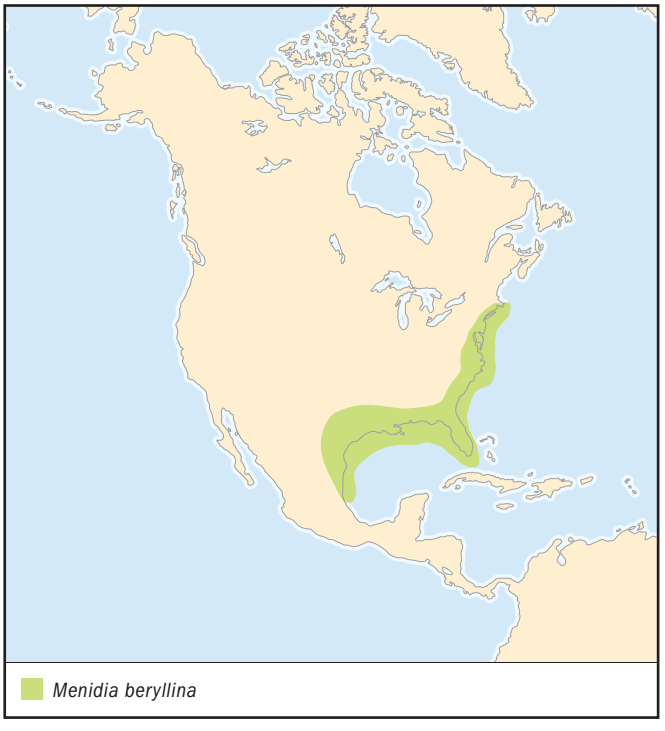
SIGNIFICANCE TO HUMANS
Collected by hand during spawning runs. ◆

Inland silverside
Menidia beryllina

FAMILY
Atherinidae

TAXONOMY
Chirostoma beryllinum Cope, 1867, Potomac River, opposite Washington, D.C., at Jackson City, Virginia, United States.

OTHER COMMON NAMES
None known.



PHYSICAL CHARACTERISTICS
Maximum length of 5.9 in (15.0 cm). Elongate, slender silverside with a fairly compressed body. Silvery lateral band, with a dark line above. Greenish dorsally and whitish ventrally. Scales are smooth to the touch.

DISTRIBUTION
Along the coast of North America from Massachusetts to northern Mexico.

HABITAT
Coastal waters as well as freshwater rivers and streams. Ascends streams and can live entirely in freshwater. Prefers sandy substrate.

BEHAVIOR
Schooling fish that can make the transition between freshwater and saltwater.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton.

REPRODUCTIVE BIOLOGY
Spawns in the spring and summer months.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Some populations have been established in freshwater impoundments to provide food for sport fishers. ◆

No common name
Rheocles derhami

FAMILY
Bedotiidae

TAXONOMY
Rheocles derhami Stiassny and Rodriguez, 2001, Ambomboa River, Madagascar.

OTHER COMMON NAMES
None known.

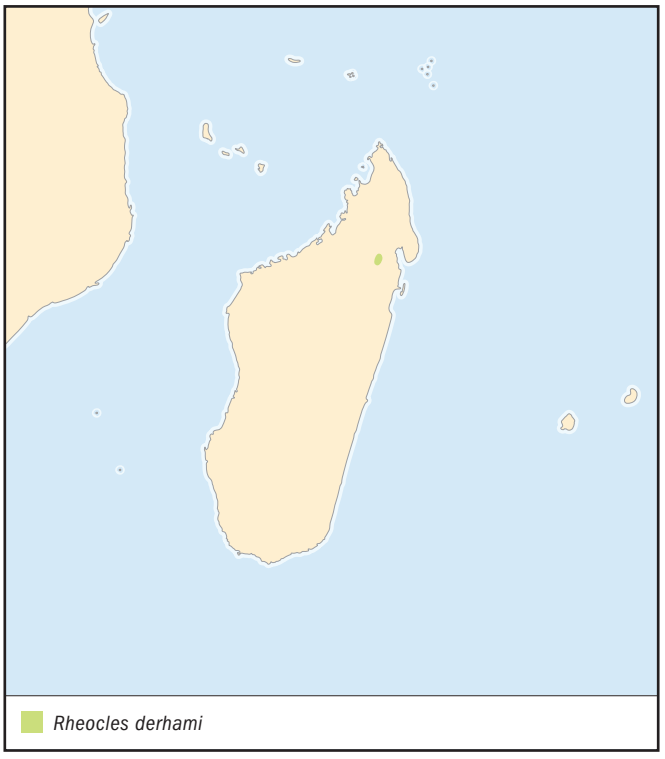
PHYSICAL CHARACTERISTICS
Grows to 1.97 in (5 cm) maximum length. Small, moderately deep-bodied fish with relatively large scales. Scales are absent from the nape, chest, and belly. Before spawning, males become darker in color, with blackish blue on the fins and orange-red around the throat; otherwise both males and females are a drab grayish tan. Males have long, filamentous second dorsal, anal, and pectoral fins; this sexual dimorphism is unique within the genus.

DISTRIBUTION
Sofia River drainage in northern Madagascar. Known from the Mangarahara River and one of its tributaries, the Ambomboa River.

HABITAT
Pools in clear streams.

BEHAVIOR
Little is known.

FEEDING ECOLOGY AND DIET
Appears to feed almost exclusively on terrestrial insects.



REPRODUCTIVE BIOLOGY
Sexually dimorphic. Spawning behavior is unknown.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Boeseman's rainbowfish
Melanotaenia boesemani

FAMILY
Melanotaeniidae

TAXONOMY
Melanotaenia boesemani Allen and Cross, 1980, Ajamaru Lakes, Vogelkop Peninsula, Irian Jaya, Indonesia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Attains 4.5 in (11.5 cm) in maximum length. Laterally compressed and deep bodied, with the head tapering to a point. A striking fish, with blue-gray coloration on the front half of the body and brilliant orange on the back half. Dorsal fins have a white margin.

DISTRIBUTION
Ajamaru Lakes region of Vogelkop Peninsula, New Guinea.

HABITAT
Clear lakes and streams.

BEHAVIOR
Shoaling fishes that feed on insects at the surface.

FEEDING ECOLOGY AND DIET
Omnivorous; prefers terrestrial insects but also feeds on aquatic insects, zooplankton, and algae.

REPRODUCTIVE BIOLOGY
Easy to breed in captivity. Eggs are laid in aquatic plants, and females produce 10–20 eggs per day, spawning daily for an extended period.

CONSERVATION STATUS
Listed as Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Very popular in the aquarium trade. In the late 1980s, before government restrictions on the fishery, 60,000 males a month were being removed from the wild to be sold as aquarium fish. While rainbows sometimes may be eaten, they are reportedly bony and have a strong formic acid taste, owing perhaps to their preference for ants as a source of food. ◆

Flower of the wave
Iso rhothophilus

FAMILY
Notocheiridae

TAXONOMY
Tropidostethus rhothophilus Ogilby, 1895, Maroubra Bay, N.S.W., Australia.

OTHER COMMON NAMES
English: Surf sardine; French: Surfette commune; Spanish: Rompeolas.

PHYSICAL CHARACTERISTICS
Grows to 2.95 in (7.5 cm) maximum length. Small, laterally compressed fish with a blunt head and a notch in the dorsal

portion of the opercle. Body is deepest around the pectoral fin base, strongly tapering posteriorly and with an abdominal keel. Scales are small, deciduous, and absent anteriorly. Coloration is translucent, with a wide, silvery midlateral band.

DISTRIBUTION
Known from eastern Australia and Taiwan, though likely found throughout Indo-West Pacific.

HABITAT
Typically, rough surf along sandy or rocky coastline; infrequently in estuaries.

BEHAVIOR
Schools in highly oxygenated surf-zone regions around rocky outcroppings or along beaches. Very delicate; does not survive handling.

FEEDING ECOLOGY AND DIET
Likely feeds on zooplankton.

REPRODUCTIVE BIOLOGY
Little is known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Rarely caught; not a fish of commercial importance. ◆

No common name

Neostethus bicornis

FAMILY
Phallostethidae

TAXONOMY
Neostethus bicornis Regan, 1916, Kuala Langat, peninsular Malaysia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Small, transparent fish, with urogenital and anal openings placed far anteriorly. Dramatic sexual dimorphism. Males have a complex, asymmetrical structure, the priapium, derived from the pectoral and pelvic girdles and used in reproduction.

DISTRIBUTION
Peninsular Malaysia, Singapore, Thailand, Borneo, Palawan (Philippines).

HABITAT
Fresh and brackish water.

BEHAVIOR
Forms small schools in shallow water near the shore.

FEEDING ECOLOGY AND DIET
Planktivorous.

REPRODUCTIVE BIOLOGY
The male violently swims into the female and knocks her onto her side, gripping her with his ctenactinia, two elongate bones that are part of the priapium. He then attaches a bolus of sperm over her oviduct and swims in rapid spirals and forward bursts that may break the surface of the water, apparently in an effort to break free from the female.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Celebes rainbowfish

Marosatherina ladigesi

FAMILY
Telmatherinidae

TAXONOMY
Telmatherina ladigesi Ahl, 1936, Makasar, Sulawesi, Indonesia.

OTHER COMMON NAMES
German: Celebes Sonnenstrahlfisch.

PHYSICAL CHARACTERISTICS
Attains maximum length of 3.1 in (8 cm). Laterally compressed and translucent, with bluish midlateral band. Fins bordered in yellow. Elongate second dorsal and anal fins.

DISTRIBUTION
Bantimurung area of south Sulawesi.

HABITAT
Lakes and streams in karst region.

BEHAVIOR
Peaceful community fish in the aquarium.

FEEDING ECOLOGY AND DIET
Omnivorous.

REPRODUCTIVE BIOLOGY
Eggs are attached by a thread to floating plants, in small numbers and over a period of several days. Spawning may last for several months; eggs develop in eight to 11 days. Males behave animatedly during courtship.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A popular aquarium species that is bred commercially in large numbers in Southeast Asia. ◆

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Robert Schelly, MA

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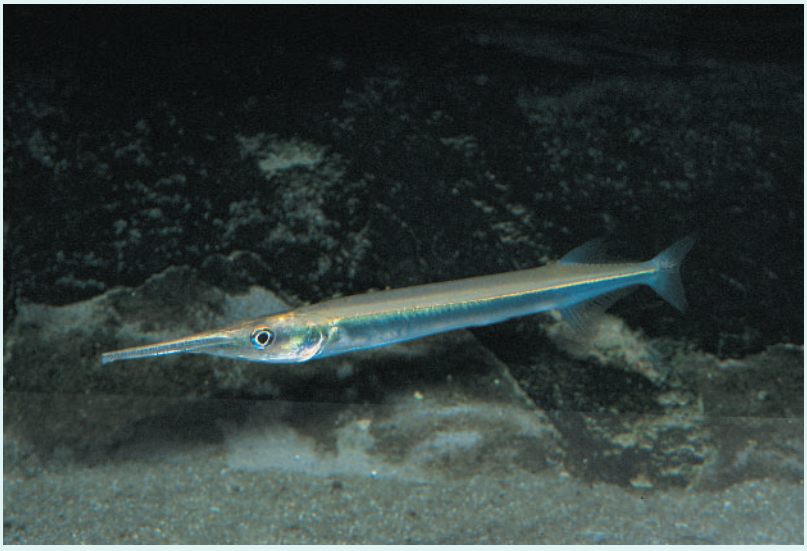
Beloniformes
(Needlefishes and relatives)

Class Actinopterygii
Order Beloniformes
Number of families 5

Photo: A silver needlefish (*Xenentodon cancila*) from Southeast Asia. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)



Evolution and systematics

The Beloniformes is one of three orders within the series Atherinomorpha. One of the other two orders, the Atheriniformes, is thought by some ichthyologists to represent an unnatural grouping of several lineages, while others consider it monophyletic (a natural group). The other order, Cyprinodontiformes, is the sister-group of the Beloniformes, as evidenced by numerous internal characters, including modifications to the gill arches and the bones surrounding the eyes. Both Cyprinodontiformes and Beloniformes are agreed to be monophyletic. Beloniformes themselves are united by derived internal characters of the gill arches rather than any conspicuous external morphological characters. Five families of fishes make up the order Beloniformes: Adrianichthyidae (ricefishes), Belonidae (needlefishes), Scomberesocidae (sauries), Exocoetidae (flyingfishes), and Hemiramphidae (halfbeaks). Within these families are 38 genera and about 200 species, 51 of which are either brackish or freshwater, the remainder of which are marine.

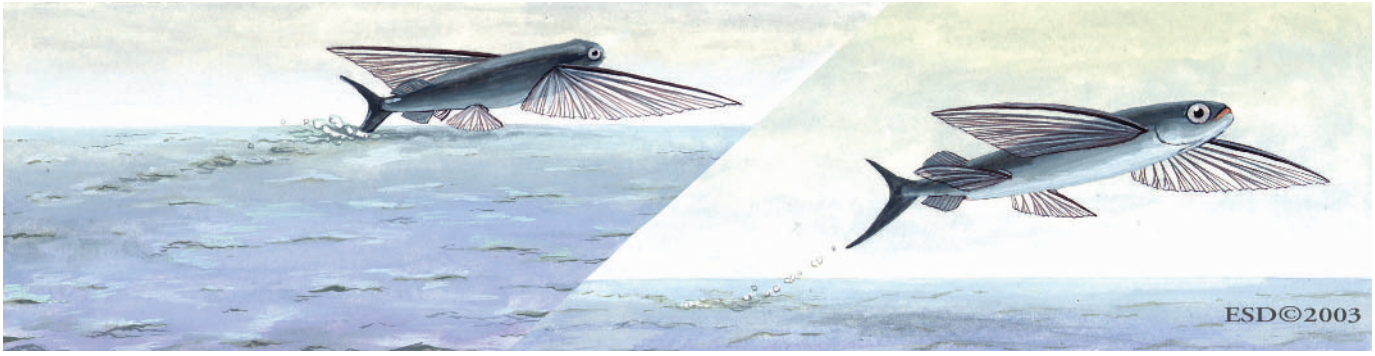
The earliest known fossil Beloniformes are just over 50 million years old, and come from two sites: the exocoetids from Monte Bolca in Italy, and the hemiramphids from the Selsey formation in England. Beloniformes are broadly divided into two suborders, the Exocoetoidei (beaked forms: belonids, scomberesocids, exocoetids, and hemiramphids) and the Adrianichthyoidei (lacking a beak; adrianichthyids). Adrianichthyids were traditionally included within the Cyprinodontiformes until Rosen and Parenti argued for their inclusion within the Beloniformes in 1981, based mainly on characters of the gill arches and hyoid apparatus. Adrianichthyids are now considered to be the sister lineage to the rest of the order, within which the sister groups Belonidae-Scomberesocidae and Hemiramphidae-Exocoetidae have been suggested.

Contrary to this scheme, a study based on morphology and molecules, published in 2000 by Lovejoy, places halfbeaks as the ancestral form among the beaked beloniforms. In Lovejoy's tree, some halfbeaks are most closely related to needlefishes and sauries, while the marine halfbeak *Hemiramphus* is sister to flyingfishes. This result refutes an old hypothesis, based on the observation that needlefishes pass through a halfbeak stage during their development, that halfbeaks derive from needlefishes via truncation of the development sequence.

Physical characteristics

Beloniformes are typically elongate fishes, with dorsal and anal fins situated posteriorly on the body and the lateral line situated ventrally. Additional characteristics of the group include fusion of the toothed 5th ceratobranchials into a lower pharyngeal jaw and an open nasal pit. Belonids, aptly called needlefishes, are sleek and garlike piscivores, with very long upper and lower jaws studded with sharp teeth. They can achieve lengths of up to 3.3 ft (1 m). A small number of needlefishes have a reduced upper jaw, and like halfbeaks, feed on plankton and insects. Scomberesocids, of which the largest are about 1.65 ft (0.5 m) long, can be distinguished from belonids by the five or six finlets behind their dorsal and anal fins. The diminutive scomberesocid *Cololabis adocetus*, at 3 in (7.5 cm), is the smallest fish in the surface waters of the open ocean.

In most species of hemiramphids, or halfbeaks, the lower jaw is much longer than the upper. The front margin of the upper jaw is triangular in shape, the scales are large and cycloid, and fin spines are lacking. Exocoetids, the flyingfishes, are torpedo shaped with greatly enlarged pectoral fins, and the lower lobe of the caudal fin is stiffened and much larger than the upper. Interestingly, the most primitive flyingfish genera, *Oxyporhamphus* (once included with hemiramphids),



The four-winged flyingfish, *Cheilopogon pinnatibarbatus* (family Exocoetidae), taxis by rapidly beating its caudal fin in the water. It then achieves free flight, for a distance up to 160 ft (50 m). (Illustration by Emily Damstra)

Fodiator, and *Parexocoetus*, have elongate lower jaws reminiscent of halfbeaks. More derived flyingfishes have acquired oversized pelvic fins in addition to large pectoral fins, and are called four-wingers.

Adrianichthyids, the most basal among the Beloniformes, are superficially unlike other members of the group. Most of the species are in the genus *Oryzias*, and are small, relatively deep-bodied fishes with large eyes, upturned mouths, and a long anal fin base. Noteworthy in the family is the duckbilled buntingi (*Adrianichthys kruyti*), which has a bill-shaped mouth with the upper jaw overhanging the lower. *Xenopoecilus* species also have a bill-shaped mouth, and the carry their eggs at the base of the pelvic fins by way of filamentous attachments.

Distribution

Beloniformes are widely distributed in temperate and tropical marine and fresh waters. Adrianichthyids are found in Asian fresh and brackish waters from India to Japan, and in the Indo-Australian archipelago. Belonids are found in the open ocean in tropical and temperate seas worldwide, with numerous species in the freshwaters of South America and some in Asia. Like marine belonids, scomberesocids are widely distributed in warmer waters of the open ocean. Exocoetids are found in warm waters of the Atlantic, Pacific, and Indian Oceans. Hemiramphids have a similar distribution in marine waters, but have also invaded freshwaters, especially in the Indo-Australian region.

Habitat

Marine beloniforms can be found in the surface waters of the open ocean, as well as in coastal habitats like estuaries and mangrove swamps. Adrianichthyids, belonids, and hemiramphids can be found in a diversity of tropical freshwater habitats, including lakes and rivers.

Behavior

One characteristic of many beloniforms is a strong attraction to lights at night. This behavior is exploited by fishermen, who use lights to capture schools of sauries that cruise just below the ocean surface. Such fishing methods, however, involve a peculiar (although infrequent) hazard: impalement by large needlefishes. In one documented case, a 3.3 ft (1 m) long *Tylosurus* fatally impaled a fisherman after jumping toward the light on board his canoe.

Certainly the most remarkable beloniform behavior is exocoetid flight. (It should be noted that flight is not entirely restricted to exocoetids: Some hemirhamphids are capable of gliding, and *Euleptorhamphus viridis* has been reported to travel 164 ft [50 m] in two jumps.) In the more derived four-winged flyingfish species, flight is achieved as follows. The fish, swimming at a speed of about 33 ft/s (10 m/s), breaks the surface at an oblique angle and taxis for 16.4–82 ft (5–25 m) by rapidly beating the caudal fin in the water. Then a free flight ensues, which may span a distance of 164 ft (50 m) and reach a height of 26.2 ft (8 m). Once the fish loses altitude, caudal fin taxiing can be repeated without returning to the water, so that flights can be stretched to distances of 1,312 ft (400 m). Intriguingly, flyingfishes seem to sense wind direction and take off into the wind, and tantalizing evidence suggests that they can control the direction of flight; *Cypsilurus* appear to successfully seek out patches of seaweed in which to land. So why do flyingfishes fly? One of the most likely hypotheses is that flight has evolved as a tactic for evading predators.

Feeding ecology and diet

Beloniformes utilize a relatively wide spectrum of foods. Most impressive perhaps are the marine needlefishes, which cruise through the surface waters of the open ocean devouring small fishes. However, not all needlefishes are piscivores. In the Amazon, many belonids feed heavily on zooplankton or insects. *Belonion apodion*, which grows only to about 2 in (5 cm), is unusual in that it deftly snaps up individual rotifers, which are less than 0.004 in (0.1 mm) long and usually pass through the gill rakers of filter-feeding planktivorous fishes. *Potamorrhaphis*, which prefers terrestrial insects (especially flying ants), hovers motionlessly and waits for prey to fall to the surface alongside its body. Then it rapidly curls the body and strikes at the prey from the side.

Freshwater halfbeaks also feed on terrestrial insects, and some are particularly well suited to this mode of feeding.

Members of the genus *Hemirhamphodon* are noteworthy for having numerous anteriorly directed teeth on their lower jaws, which ensnare ants and other insects found floating on the surface. Marine halfbeaks, on the other hand, tend to feed on algae, diatoms, and sea grasses, though some species eat small fishes. Planktivorous marine beloniforms include the flyingfishes and sauries. Ricefishes are omnivorous and will eat plankton, small insects, detritus, and plant material.

Beloniformes themselves often fall prey to larger fishes. Flyingfishes in particular are eaten by mackerel, tuna, and marlin, among other predatory fishes, as well as squids and birds.

Reproductive biology

Much of what is known about beloniform reproductive biology involves the eggs and larvae. Typically, eggs develop in one to two weeks, and the larvae are immediately able to feed upon hatching. Many pelagic beloniform eggs have filamentous projections that cause them to stick to floating debris. Needlefish eggs have tendrils that are particularly sticky, and they form egg clusters that stick to other objects in the water. Likewise, sauries produce filamentous eggs that float in open water, but they are less adhesive than needlefish eggs. Flyingfishes lay pelagic eggs that may or may not have filaments, and some species attach their eggs to floating seaweed. Marine halfbeaks lay eggs with tendrils that float about in open water, but some freshwater representatives bear live young, namely *Dermogenys*, *Nomorhamphus*, and *Hemirhamphodon*. In these viviparous forms, long genital papillae are used for internal fertilization, and the male anal fin is modified into an andropodium.

The adrianichthyid *Horaichthys* from India, uniquely among atherinomorphs, produces encapsulated sperm bundles, or spermatophores. In adrianichthyids other than *Oryzias*, fertilization is apparently internal. The eggs of many species of adrianichthyids are retained externally by the female for various lengths of time. Females of the species *Xenopoecilus oophorus*, known as the egg-carrying buntingi, carry a cluster of about 30 fertilized eggs attached by filaments in an external concavity near the vent. The pelvic fins cover and protect this egg mass.

Conservation status

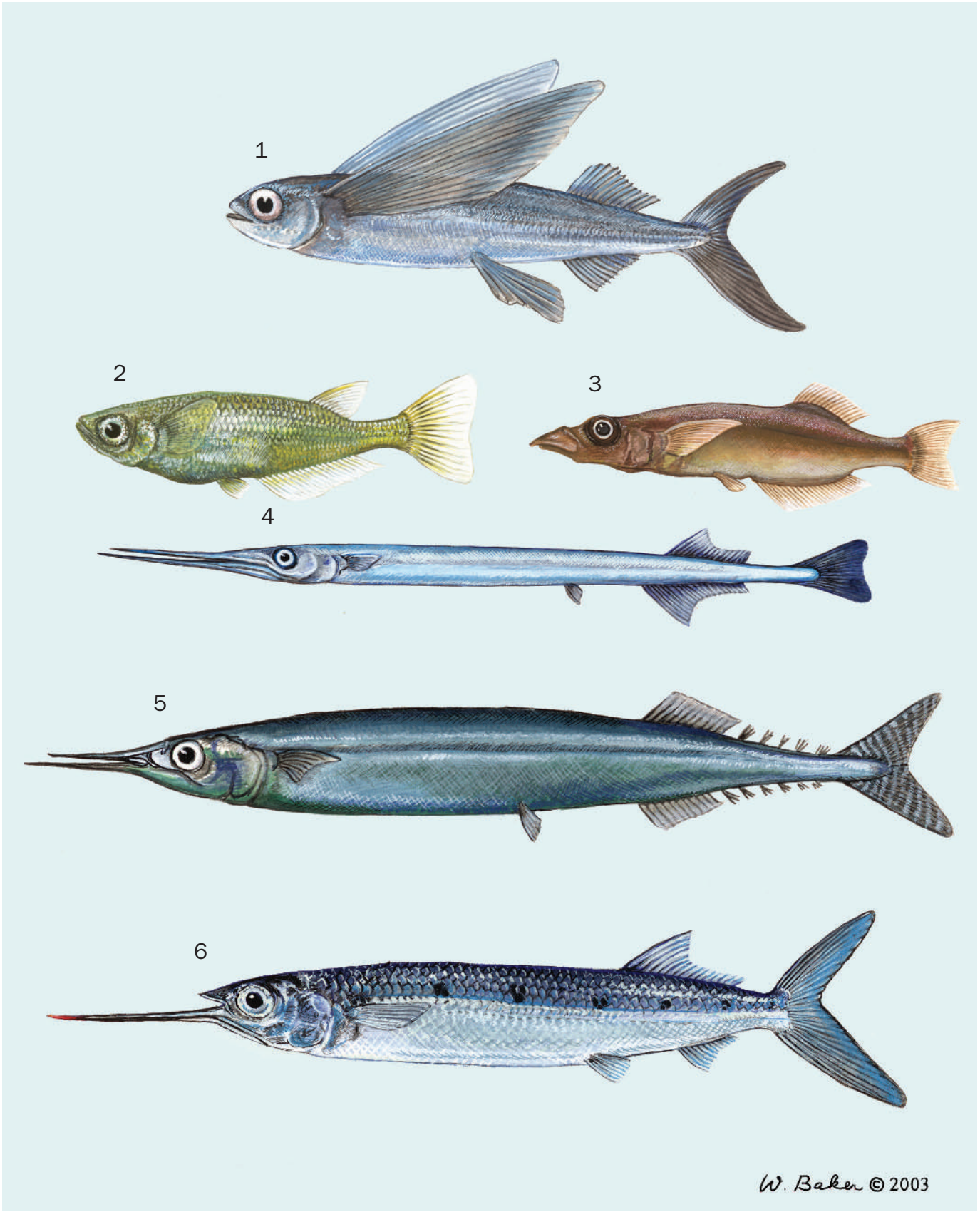
No Beloniformes are CITES listed, or listed as endangered by the U. S. Fish and Wildlife Service. However, 16 species are included on the IUCN Red List. Eight of those, mostly *Oryzias* species, are categorized as Vulnerable, one species is listed as Lower Risk/Near Threatened, and two species are listed as Data Deficient. Three species are listed as Endangered: *Oryzias orthognathus*, *Xenopoecilus oophorus*, and *Xenopoecilus sarasinorum*. Listed as Critically Endangered are *Adrianichthys kruyti* and *Xenopoecilus poptae*, both of which are known only from Lake Poso, Sulawesi. Although no Beloniformes are formally listed as Extinct in the Wild by the U. S. Fish and Wildlife Service or Extinct by the IUCN, *Adrianichthys kruyti* is generally thought to be extinct. Pressure from an introduced species of catfish, in addition to parasites that entered the lake with the catfish, are implicated in the decline of the Lake Poso adrianichthyids.

Significance to humans

Many Beloniformes are fished at night using lights, and some rather creative methods have been devised. Where flyingfishes are abundant, fishermen that leave a light suspended all night over a canoe partially filled with water can return in the morning to a boat full of fresh fish. The fish are drawn to the light and jump into the canoe, but have too little water to jump back out. Flyingfishes are also attracted to leaves or straw scattered about the surface as a place to lay their eggs, and can be fished by using such material.

Some Beloniformes are used by humans as more than just food. Numerous freshwater species, including halfbeaks, ricefishes, and needlefishes, can be found in the aquarium trade. In Thailand, the halfbeak, *Dermogenys pusillus*, is bred in captivity so that males, which will engage rivals by locking jaws, can be used as fighting fish. Members of the genus *Oryzias* are propagated in large numbers in captivity to be used in experimental research.

Finally, it should be mentioned that needlefishes can in rare cases be traumatogenic, causing injury or death by means of impalement. In one such case, a hapless surfer was killed when the snout of a fast-swimming needlefish went through his eye socket and into his brain.



1. California flyingfish (*Cheilopogon pinnatibarbatus californicus*); 2. Japanese rice fish (*Oryzias latipes*); 3. Duckbilled buntingi (*Adrianichthys kruyti*); 4. Californian needlefish (*Strongylura exilis*); 5. Atlantic saury (*Scomberesox saurus saurus*); 6. Blackbarred halfbeak (*Hemiramphus far*). (Illustration by Wendy Baker)

Species accounts

Japanese rice fish
Oryzias latipes

FAMILY
Adrianichthyidae

TAXONOMY
Poecilia latipes Temminck and Schlegel, 1846, Japan.

OTHER COMMON NAMES
English: Japanese medaka, tooth-carp; German: Japan-Reiskärpfling; Cantonese: Fut mei dzeung ue; Japanese: Medaka.

PHYSICAL CHARACTERISTICS
Maximum length 1.6 in (4 cm). Small and shallow bodied, with upturned mouth and silvery olive coloration. No spines in dorsal or anal fins. Many strains of captive-raised Japanese rice fish have been selectively bred for pale yellow color. Strains that appear red or mottled black and gold have also been developed.

DISTRIBUTION
Japan, Korea, China, and Vietnam, as well as the great rivers of Southeast Asia: the Mekong, Red, Irrawaddy, and Salween.

HABITAT
Calm stretches of streams, rice paddies, and wetlands.

BEHAVIOR
Forms schools, generally peaceful.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton and insects, as well as some detritus and plant material.

REPRODUCTIVE BIOLOGY
Fertilization is external, although the eggs are carried for a short time, stuck to the female's abdomen, prior to deposition. Females can produce broods of 10–40 eggs every two days during the breeding season. Eggs are slightly larger than 0.039 in (1 mm) in diameter and usually hatch in 8–14 days.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Used widely in experimental research, also found in the aquarium trade. ◆

Duckbilled buntingi
Adrianichthys kruyti

FAMILY
Adrianichthyidae

TAXONOMY
Adrianichthys kruyti Weber, 1913, Lake Poso, Sulawesi, Indonesia.

OTHER COMMON NAMES
English: Duckbill Poso minnow; German: Entenschnabelkärpfling.

PHYSICAL CHARACTERISTICS
Maximum length about 4.3 in (11 cm). Large, horizontal, duck-bill shaped mouth, with upper jaw overhanging lower; eyes large, extend beyond dorsal head-profile when viewed from side. Elongate, somewhat compressed.

DISTRIBUTION
Lake Poso, Sulawesi.

HABITAT
Deeper waters of Lake Poso.

BEHAVIOR
Unknown.

FEEDING ECOLOGY AND DIET
Unknown.

REPRODUCTIVE BIOLOGY
Unknown, though one specimen reported to be a hermaphrodite.

CONSERVATION STATUS
Listed as Critically Endangered on the IUCN Red List; Harrison and Stiassny (1999) think it possibly extinct.

SIGNIFICANCE TO HUMANS
Kottelat reported that the adrianichthyids he observed were heavily parasitized by copepods; native fisherman say these parasites became a problem when *Clarias* was introduced into Lake Poso in the early 1980s. Voracious snakeheads have also been introduced into the lake, and may have led to the decline

of the endemic fishes. He argues that the duckbilled buntingi may not be extinct, but just no longer abundant enough for fisherman to expend effort and so never observed. Whatever its status, *Adrianichthys kruyti* is an example of an endemic species important as a fishery declining dramatically following exotic species introductions by humans. ◆

Atlantic saury
Scomberesox saurus saurus

FAMILY
Scomberesocidae

TAXONOMY
Esox saurus Walbaum, 1792, Cornwall and British seas.

OTHER COMMON NAMES
English: Atlantic needlefish; French: Aiguille de mer; German: Echsenhecht; Spanish: Alcrique.

PHYSICAL CHARACTERISTICS
Maximum length 19.7 in (50 cm). Elongate and needlefish-like, but with toothless jaws and finlets following the dorsal and anal fins.

DISTRIBUTION
Mediterranean, North Atlantic, rarely Iceland, Norway, Denmark.

HABITAT
Surface waters of the open ocean.

BEHAVIOR
Schooling fishes that travel long distances through the open ocean. Spawn in warmer waters, migrate to plankton-rich temperate waters to feed. Leap out of the water when pursued by predators.

FEEDING ECOLOGY AND DIET
Zooplankton and fish larvae.

REPRODUCTIVE BIOLOGY
External fertilization, eggs scattered in open water.

CONSERVATION STATUS
Not threatened.

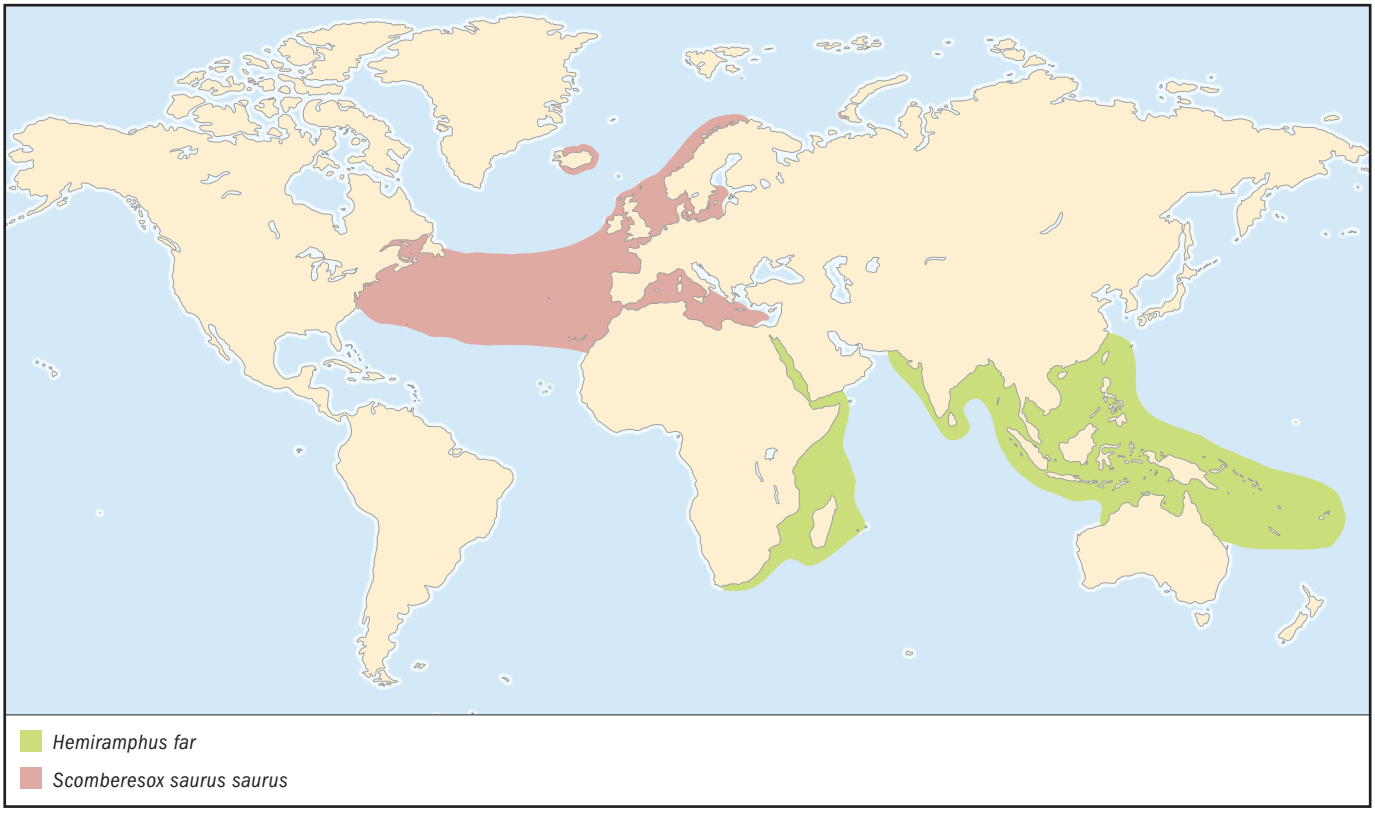
SIGNIFICANCE TO HUMANS
Said to have delicious flesh, but not abundant enough to support a large fishery. ◆

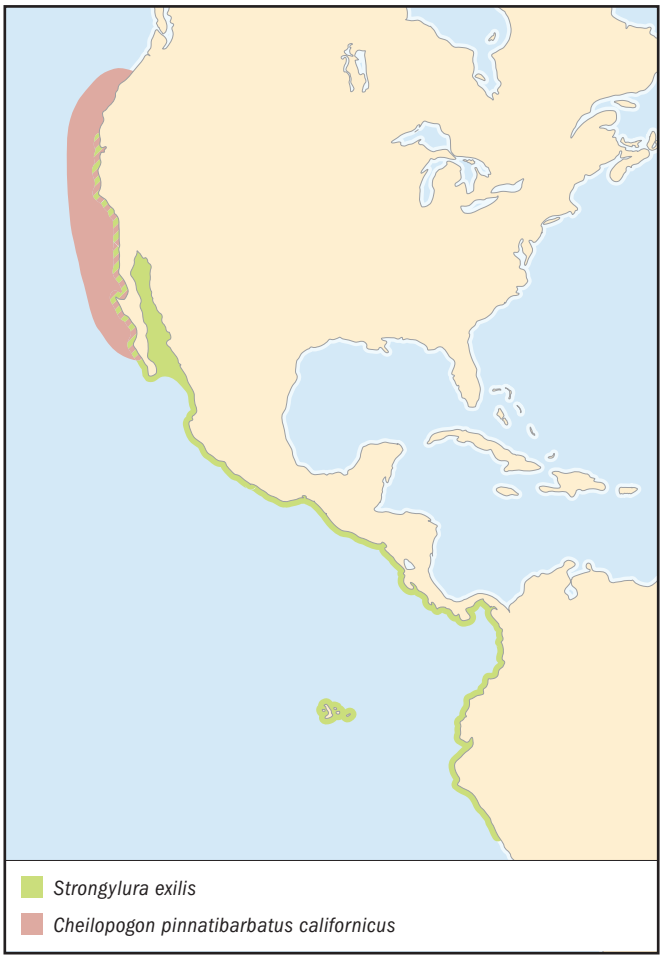
Californian needlefish
Strongylura exilis

FAMILY
Belonidae

TAXONOMY
Belone exilis Girard, 1854, San Diego, California.

OTHER COMMON NAMES
French: Aiguille de Californie; Spanish: Agujón bravo de California.





PHYSICAL CHARACTERISTICS
Maximum length 35.8 in (91 cm). Very elongate, with long snout and sharp teeth. Emarginate caudal fin, no dorsal or anal fin spines.

DISTRIBUTION
Coastally from San Francisco to Peru; also in the Galápagos.

HABITAT
Lagoons, harbors, and coastal areas. Frequents mangroves and enters freshwaters.

BEHAVIOR
Sometimes schools in large numbers, leaps out of the water when threatened.

FEEDING ECOLOGY AND DIET
Feeds on small fishes.

REPRODUCTIVE BIOLOGY
Eggs are attached to floating vegetation by means of long filaments; larvae drift in surface waters. The eggs are approximately 0.14 in (3.5 mm) in diameter and hatch in about two weeks. Larvae are 0.35–0.47 in (9–12 mm) at hatching.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sold fresh in fish markets. In very rare cases, may cause injury or death by impalement. ◆

Blackbarred halfbeak
Hemiramphus far

FAMILY
Hemiramphidae

TAXONOMY
Esox far Forsskål, 1775, Luhaiya, Yemen, Red Sea.

OTHER COMMON NAMES
English: Blackbarred garfish; French: Aiguillette, demi-bec bagnard.

PHYSICAL CHARACTERISTICS
Maximum length 17.7 in (45 cm). Lower jaw beaklike and dramatically longer than upper jaw; color is bluish dorsally and silvery on sides, with three to nine vertical bars. Dorsal and anal fins posteriorly situated, lower lobe of caudal fin longer than upper.

DISTRIBUTION
Indo-West Pacific: Red Sea and East Africa to Samoa, from northern Australia and New Caledonia to the Ryukyu Islands. Has entered the eastern Mediterranean through the Suez Canal.

HABITAT
Marine; near vegetation in coastal areas.

BEHAVIOR
Forms schools.

FEEDING ECOLOGY AND DIET
Feeds mostly on sea grasses, in addition to green algae and diatoms.

REPRODUCTIVE BIOLOGY
Spawns in estuaries.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Commercially fished, said to have good-tasting flesh, sometimes used as bait. ◆

California flyingfish
Cheilopogon pinnatibarbatus californicus

FAMILY
Exocoetidae

TAXONOMY
Exocoetus californicus Cooper, 1863, Santa Catalina Island, California.

OTHER COMMON NAMES
French: Exocet californien; Spanish: Volador de California.

PHYSICAL CHARACTERISTICS
Maximum length 15 in (38 cm). One of the "four-winged" flyingfishes; both pectoral and pelvic fins are enlarged. Lower lobe of caudal fin is also considerably larger than the upper. Bluish gray dorsally, silver ventrally.

DISTRIBUTION
Oregon to southern Baja California.

HABITAT
Surface waters of the open ocean.

BEHAVIOR
Schooling fishes, capable of leaping out of the water and gliding for long distances, possibly as a means of evading predators.

FEEDING ECOLOGY AND DIET
Zooplankton and small fishes.

REPRODUCTIVE BIOLOGY
Spawns in the summer months. Eggs are pelagic, and stick to floating seaweed and other debris. The eggs are approximately 0.07 in (1.8 mm) in diameter. Larvae are roughly 0.17 in (4.5 mm) long at hatching.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Occasionally used as bait. ◆

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Robert Schelly, MA

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Cyprinodontiformes
(Killifishes and live-bearers)

Class Actinopterygii
Order Cyprinodontiformes
Number of families 9

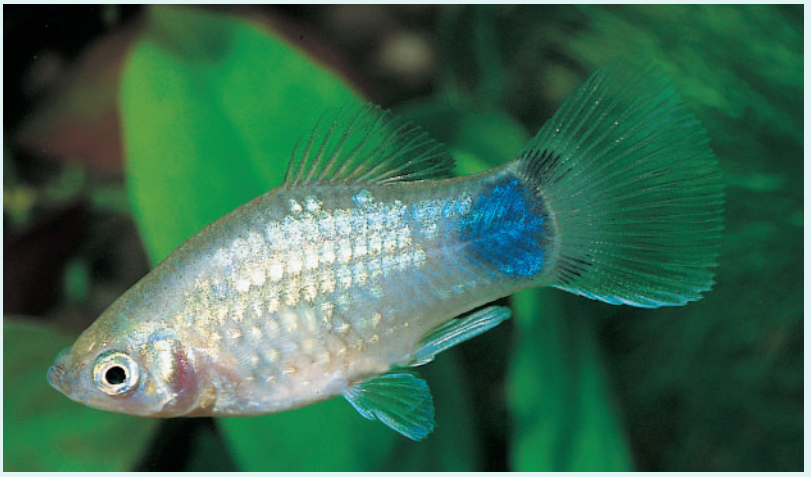

Photo: A male blue platy (*Xiphophorus maculatus*) from Central America. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

As early as 1828 Wagner recognized a suprageneric category for the group known to us today as the Cyprinodontiformes. In 1835 Agassiz erected the Cyprinodontes as the family containing the genera *Cyprinodon*, *Lebias*, *Molinesia* (correctly spelled *Mollienesia*), *Poecilia*, and *Anableps*. By 1883 the term Cyprinodontidae was in general use for 30 genera and 130 species, as reflected in the work of Jordan and Gilbert. In his classic work *The Cyprinodonts*, published in 1895, Garman arranged the many genera of the Cyprinodontes into eight subfamilies, and while he erroneously included the characin genus *Neolebias* and the cyprinid genus *Fundulichthys*, his systematic view of the constituents of the Cyprinodontiformes is about the same today. This is reflected in the work of Berg, who formally erected the group as the order Cyprinodontiformes in 1940.

In 1964 Rosen placed the Cyprinodontiformes in the superfamily Cyprinodontoidea in the order Atheriniformes. As of 2002 the Cyprinodontiformes were considered a natural group (i.e., a monophyletic group) most closely related to the Beloniformes, the order containing halfbeaks, medakas, needlefishes, sauries, and flyingfishes. Rosen took Garman's eight subfamilies and ordered them into five families, the Cyprinodontidae for all the oviparous genera, the Anablepidae for the viviparous genus *Anableps*, the Jenynsiidae for the viviparous genus *Jenynsia*, the Goodeidae for the genera of the viviparous splitfins, and the Poeciliidae for the viviparous genera with gonopodium. In 1924 Hubbs had argued for the placement of *Anableps* and *Jenynsia* into the family Anablepidae, a view not adopted by Rosen. The five families of Rosen correspond today to the order Cyprinodontiformes. In Rosen's work there was a clearly defined family-level separation of the lineages into viviparous and oviparous. Essentially, the five families were thought to be related, but there were no proposals about the details of the relationships among the five families or their genera.

It was not until the iconoclastic work of Parenti in 1981 that relationships for the cyprinodontiform genera and their families were proposed. Shared derived characters (evolutionary novelties), not primitive characters, were used to define the various evolutionary lineages in a systematic phylogenetic analysis of the order. Almost all the known genera were reevaluated, and a comprehensive cladogram was constructed to illustrate the proposed interrelationships of the genera and the families into which they were placed. For the first time the order Cyprinodontiformes was defined using only derived characters, consisting of a suite of various osteological features and, in general, a long developmental period and early breeding habits. In the new ordering the viviparous families did not form a monophyletic group, because some live-bearers turned out to be related more closely to oviparous species than to other live-bearers. There were numerous taxonomic and nomenclature changes as the result of the restructuring of the genera as well as the proposed scheme of their relationships.

Three taxonomic arrangements were proposed, wherein viviparous genera were deemed to be sister taxa to oviparous genera. This kind of relationship had not been contemplated previously and constituted a paradigm shift within cyprinodontiform systematics. The viviparous genera *Anableps* and *Jenynsia* were recognized as sister taxa because of shared characters in their reproductive biology. These, in turn, were considered the sister group of the oviparous *Oxyzygonectes*, which had been aligned with *Fundulus*. These genera constitute the Anablepidae. The viviparous family Goodeidae, with 17 genera, commonly known as splitfins, was realigned with the sister group formed by the oviparous genera *Crenichthys* and *Empetrichthys*. This group now constitutes the family Goodeidae, which may be considered to have two subfamilies, the Goodeinae and the Empetrichthyinae. The Poeciliidae, with 27 genera, was placed in a clade with the oviparous African lampeyes, *Aplocheilichthys*, and its related genera and the

Pacific foureyed fish (*Anableps dowi*) from Central America. (Photo by William E. Townsend, Jr./Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

oviparous genus *Fluviphylax*. That group, in turn, was hypothesized to be the sister group of the Anablepidae.

As a result of these revisions, the killifishes, that is, the oviparous cyprinodontiform genera, are no longer considered to constitute a monophyletic group in the scientific sense, but in the vernacular the term is used commonly. It also should be noted that the Cyprinodontiformes were subdivided into two suborders, the Aplocheiloidei and Cyprinodontoidei, both of which spanned the continents of South America and Africa, with interesting zoogeographical implications.

Four major revisions of the Cyprinodontiformes have been published since 1981. Using both molecular and osteological methods, overall cyprinodontiform taxonomy was revisited, the phylogenetic relationships of the Old World and New World aplocheiloids were revised sharply, and a major restructuring of the Poeciliidae was undertaken. An additional molecular study of the phylogeny of the family Rivulidae and its two subfamilies, the Rivulinae and Cynolebiatinae, was published in 1999, and this may lead to a radical taxonomic and nomenclatural revision of these two subfamilies.

The fossil record does little to illuminate cyprinodontiform origins. The earliest fossils, the cyprinodontid *Pachylebias* and *Prolebias*, both found in Europe, date to the Oligocene epoch, 25–40 million years ago (mya). Most fossils date to the Miocene, 10–25 mya. The fossil record is relatively recent compared with the inferred history of the Cyprinodontiformes. The phylogenetic relationships of recent killifishes and live-bearers accord well with the realities of plate tectonics and the breaking up of Gondwana, the single supercontinent formed by present-day South America, Africa, Antarctica, Australia, New Zealand, Madagascar, and India plus an assortment of other small plates not part of the continent of Laurasia, which was positioned to the north of Gondwana.

The distribution of the Cyprinodontiformes on today's widely separated pieces of Gondwana argues for a very ancient origin of this order of fishes, more than three times the age of the oldest-known fossil killifishes. The killifishes and live-bearers originated on Gondwana and were contemporaneous with the dinosaurs. Plate tectonics (continental drift) carried these freshwater fishes to their present locations on a journey that began with the breakup of Gondwana 140 mya. The mountain killifishes, genus *Orestias*, found in the Altiplano regions of Peru, Bolivia, and Chile, were in place long before the rising of the Andes lifted them to their lofty positions. In general, one can expect some dispersal within zoogeographical areas, but the distribution of freshwater fish families is a result mainly of continental drift.

Before plate tectonic theory, freshwater fish distributions presented great puzzles, the answers to which were sometimes fanciful speculations. For instance, both the African killifish genus *Aphyosemion* and the South American killifish genus *Rivulus* were placed in the same subfamily, the Rivulinae. If one thinks of the continents as always being in the same positions, how can the freshwater fishes of these two continents possibly be related, since there is no way small freshwater fishes can swim from Africa to South America? One of the more fanciful hypotheses, ludicrous by today's more sophisticated standards, was that a series of islands spanned the Atlantic Ocean from South America to Africa. The freshwater fishes supposedly swam from island to island, thus accounting for the separation of their families. Then the islands conveniently disappeared without a trace. Another theory held that the continents had moved apart because the earth was expanding. (Two marks on a balloon grow farther apart as the balloon is inflated.) That theory suffers from a lack of any plausible mechanism, although in its early days the theory of continental drift was subjected to the same criticism, a criticism that was answered by the now widely accepted hypotheses of seafloor spreading and subduction.

The systematics of the cyprinodontoid family Poeciliidae parallels the biogeographical situation outlined for the aplocheiloid genera *Rivulus* and *Aphyosemion*, since part of the Poeciliidae is South American and part is African. There, too, plate tectonics offers a satisfying explanation of the biogeography of that group.

The taxonomic evaluation of the Cyprinodontiformes is far from complete, and one may reasonably expect many more far-reaching revisions. Many new cyprinodontiform species are being described and will enrich our understanding of this order. In 2000 Lazara pointed out that the number of species described since the first killifish was cited in 1766 by Linnaeus has increased exponentially.

Physical characteristics

The earliest known killifish "description" is a 600-year-old piece of mother-of-pearl jewelry, one inch long, produced by the Native American Mogollon culture in the recognizable shape of *Cyprinodon tularosa*, endemic to New Mexico. As a general rule, killifishes and live-bearers are sexually dimorphic and dichromatic. In 1881 Steindachner described male and female *Cynolebias bellottii* as two different species, the female named appropriately *Cynolebias maculatus*. Cyprinodontiform males and females differ in shape and color and sometimes in numbers of anal and dorsal fin rays, as noted by Steindachner. There is a gestalt to the Cyprinodontiformes

that is difficult to describe (because they are so variable) but which makes them instantly recognizable. Few fishes can be mistaken for a killifish or live-bearer, but some of the very few are the mudminnows of the Umbridae. In fact, in 1843 *Umbra pygmaea* was described by Ayres as a killifish (*Fundulus fuscus*). Ayres was perhaps the first person to document his confusion about this resemblance.

The Cyprinodontiformes vary greatly in length, from 0.4 in (1 cm), which meets the formal definition of a miniature fish, to nearly 13 in (33 cm). Many are basically cylindrical in shape, with tapering around the caudal peduncle. Some are sleek, pike-like predators and others elongate and flat-topped (the top minnows of the order), with mouths designed for surface feeding. Some are laterally compressed and elongate for fast movement in streams or in pelagic conditions, and others that occupy benthic ecological niches may or may not be compressed but tend to be deep-bodied. Some *Orestias* have "chunky" body proportions akin to those of various fancy goldfish.

Cyprinodontiformes possess only one dorsal fin, which has its origin anywhere from far forward of the first anal fin ray to a point over the last few anal fin rays. The dorsal fin is never completely ahead and rarely entirely behind the anal fin; there almost always is an overlap. The origin of the anal fin ranges from about the midbody to three-fourths of the way from the snout. Fin rays are soft; Cyprinodontiformes do not have spines. Unpaired fins are rounded, truncated, pointed, elongated, or a combination of these shapes. Caudal fins are sometime lyre-shaped. The unpaired fins may carry very elaborate extensions or filaments, which in some cases extend beyond the caudal fin. Males of most species have contact organs, that is, bony outgrowths along the outer margins of the scales, along the fin rays, or on the snout. These organs help initiate spawning or position the males during spawning. In the live-bearers and some killifishes, the anal fin of the male becomes a gonopodium, which is used as an intromittent organ.

Pelvic fins sometimes are a prominent feature, but mostly they are small, tiny, or absent. Pelvic fin position varies, though usually it is close to the origin of the anal fin; sometimes it is far forward and close to the pectoral fins. There is no lateral line system along the sides, although in some species neuromasts protrude through the scales, running along what normally would be the course of the lateral line. The lateral line system is present around the head, with the cephalic neuromasts either totally exposed or in canals or a combination of the two states. Derived states of the cephalic lateral line system are very useful in taxonomic studies. Some species use the cephalic lateral line system to locate surface prey by its vibrations.

In 1949 Gosline developed an elaborate and very useful classification and numbering system for the sensory canals and pores of the cyprinodontiform head. The anterior naris is tubular in the aplocheiloids and in the cyprinodontoid genera *Cubanichthys* and *Anableps*. Among the cyprinodontoids this is considered to be independently derived. Overall squamation is complete, partial, or absent. There has been some attempt, mainly among those studying aplocheiloids, to use the pattern of scales on the head as a taxonomic tool. Upper and lower jaw teeth are spatulate, unicuspid, bicuspid, or tricuspid or have various combinations of those tooth forms. Sometimes teeth

The largescale foureyes (*Anableps anableps*) sees well both above and below the water because its eyes have two regions of retina, one for seeing above water and the other for underwater. It feeds on both insects from the air and small fish from the water. (Photo by Dr. Paul A. Zahl/Photo Researchers, Inc. Reproduced by permission.)

are present on the vomer. Jaw teeth are used to seize food items; teeth on the pharyngeals do the chewing. Mouths are protrusile. In some cases the lower jaw has a marked upward turn, sometimes almost perpendicular to the body axis. Some species have thickened lips to facilitate the eating of algae.

Body proportions and fin lengths and shapes are different in the sexes. Females typically have a more rounded appearance. Aquarists never have problems determining the sex of the Cyprinodontiformes. In other groups, this is not the case. Color differences are always noticeable and, in many cases, dramatic. The females generally are plain—perhaps silvery, olive drab, or brownish—whereas males may be brightly colored in crimson, iridescent greens and blues, bright yellow, bright blue, or a combination constituting a veritable riot of colors.

Distribution

Killifishes have a worldwide distribution, except for Australia, Antarctica, and Europe north of the Pyrenees and the Alps, with the exception of *Aphanius fasciatus* along the Mediterranean coast of France. Live-bearers are found in North, Central, and South America and the Caribbean.

Habitat

The Cyprinodontiformes occupy such diverse habitats that it is impossible to characterize them in a simple way. A small number of species occur in marine environments, some are brackish water species, and others are even found in hypersaline waters. Most species, however, inhabit freshwater. Many species, particularly in the genera *Aphanius* and *Cyprinodon*, are found in hypothermal environments at temperatures close to their upper lethal limit. Many *Rivulus* are semiterrestrial and may occur under leaves or logs or move overland from puddle to puddle, pond to pond, and rivulet to rivulet. In some tropical forest areas they are not to be seen until a light rain fills up tire tracks, forms puddles, or fills in the hoof

A Mombasa killifish (*Nothobranchius guentheri*) from Kenya. (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

prints of cows or the footprints of people. Presumably, they are waiting out drier conditions under damp leaf litter until there is enough water in their microhabitats. In small streams they are found along the edges in tiny pockets of water or hidden under the vegetation or stuck on leaves overhanging the water. At least one species, *Rivulus marmoratus*, inhabits land crab burrows.

Killifishes and live-bearers are found in slow-moving to fast-moving streams, tiny rivulets, shallow sheets of flowing water, puddles, ponds, rivers, lakes, swamps, salt marshes, estuaries, tidal flats, marine coastal waters, isolated desert springs, hypersaline lakes, and springheads. Where the habitats are large, they tend to be at the margins–with some notable exceptions, such as the pelagic lacustrine species. Almost all of these habitats are heavy with vegetation. Some fishes are found in areas where there are seasonal torrential conditions, which they manage to survive. Perhaps some of the semiterrestrial species leave the water under these conditions. Pelagic forms, while not common, do occur in the high-altitude lakes of the Andes and in some African lakes, most notably, Lake Tanganyika. In both Africa and South America, aplocheiloid killifishes have successfully colonized habitats with seasonal temporary waters. These species lay eggs in the substrate and die off when the water evaporates. The eggs, protected by the substrate, go into a resting state called "diapause." At times the substrate becomes so dry and cracked that it is difficult to imagine that the eggs can survive. When the rains of the wet season fill the shallow pans (in Africa, some are elephant watering holes), roadside ditches, culverts, meadows, temporary swamps, depressions, and ponds that these species inhabit, most but not all eggs hatch within hours, thereby providing a hedge against the false onset of a rainy season. Ironically, in many areas of South America and Africa human intervention in the form of road construction and its associated culverts and ditches has helped these species. Even though some places have two rainy seasons a year, this seasonal characteristic is termed "annualism."

Behavior

Males of the seasonal fishes are aggressively territorial, defending their breeding sites against other males. In aquaria, where retreat is limited, males may fight until one or both die from their injuries. Aggressive territorial behavior is common in the Cyprinodontidae and is known in the Fundulidae (*Fundulus catenatus*, *F. diaphanus*, and *Lucania goodei*). Aggression sometimes extends to nonbreeding females. Male agonistic behavior is very common among the killifishes and some live-bearers and is not necessarily territorial. In the cyprinodontids aggression is associated with the defense of breeding territories; otherwise they move about in peaceful schools. In one cyprinodontid species, *Jordanella floridae*, the male defends a territory, builds a nest, and fans the eggs—a rare case of cyprinodontiform male parental care. The long-term defense of a breeding territory by most male *Cyprinodon* likewise confers a degree of protection to the eggs deposited there.

The Poeciliinae, Anablepidae, and Goodeidae are active, gregarious, and sometimes scrappy. When they are not occupied by feeding activities, males posture and display as they seek to mate. Female receptivity behavior is complex. Among the poeciliines, a male sometimes rushes in quickly, thrusting his gonopodium, and then beats a hasty retreat, particularly in those species where the female is much larger. Poeciliine females release a pheromone-like substance, thought to be estrogen, which stimulates males into a mating frenzy. Among the goodeids, members of the genus *Allodontichthys* behave much like North American darters. In Africa the nonseasonal killifishes inhabit swamps, trickles, very small streams, and occasionally rivers, but usually they occur in vegetation-choked portions at the edges. Here they are distributed singly in small pockets of open water in the weedy margins, under the vegetation itself, or sometimes under the leaf litter on the bottom but never out in the open. Interestingly, one of these species, *Aphyosemion franzwerneri*, also behaves like a darter. In aquaria, males of all these species range from peaceful to ferociously aggressive toward each other. Those species that exhibit schooling behavior occur exclusively in the suborder Cyprinodontoidei in the families Fundulidae, Cyprinodontidae, Anablepidae, and Poeciliidae. Whether a single species or a mix of species, these schools sometimes are composed of massive numbers of individuals.

Feeding ecology and diet

Cyprinodontiformes are piscivorous, omnivorous, herbivorous, or dedicated to particular food items, such as terrestrial and aquatic invertebrates, zooplankton, detritus, algae, and vascular plants. Some are aggressive feeders and pose a danger to other species when they are introduced outside their natural range. The diet of some species in the Poeciliinae includes a significant cannibalistic component.

Reproductive biology

In the poeciliines, as the male matures, the anal fin is modified into a gonopodium; at the juvenile stage there is no difference between the male and female anal fin. The gonopodium serves as a launching platform for sperm bundles called "spermatozeugmata." In mating the gonopodium is swung forward in a vertical plane and thrust at the female genital opening so as to deposit the sperm bundles either near

or inside the opening. The end of the gonopodium has hook-like structures to facilitate the transfer of the spermatozeugmata. It is not known how the bundles are transported to the tip of the gonopodium. Females can store sperm for extended periods of time. Some females are capable of superfetation, that is, they have the ability to carry more than one brood of embryos at different stages of development. There are two gestation extremes: in type 1 the embryo is nourished by the yolk reserves laid down before fertilization ("lecithotrophy"); in type 2 the egg is very small, without much yolk, but the embryo is heavily nourished by maternal fluids transferred by a kind of placenta ("matrotrophy"). There are various intergrade levels of maternal nourishment, depending on the species. In *Tomeurus gracilis*, the egg is expelled, and development is external and dependent on the yolk reserve. This exceptional situation is, in reality, an extreme form of type 1 gestation. For the rest of the species with a gestation period, birth is initiated by muscular contractions that rupture the follicular walls of the embryos, thus initiating their exit into the environment.

There are two unisexual poeciliine "species," the all-female *Poecilia formosa* and *Poeciliopsis monacha-lucida*. Both so-called species are considered to be of hybrid origin, and some taxonomists do not regard them as true species. Matings are needed to cause these "species" to reproduce. In *P. formosa* paternal DNA is excluded, and the mating results in an all-female brood. In *Poeciliopsis*, paternal DNA is not excluded, but the resultant brood is also all female. The origins and relationships of unisexual poeciliines were reviewed by Schultz.

Males of the live-bearing anablepids, the genera *Anableps* and *Jenynsia*, have a tubular gonopodium that is used to transfer free spermatozoa, not sperm bundles, to the female. In *Anableps dowi* sperm bundles are formed but break apart before they make their way down the gonopodium. The gonopodia in these genera swing forward in a horizontal plane but only to one side, the left or the right. The vents of females are accessible only from the left or the right. Thus, left-sided males must mate with right-sided females and vice versa. Embryos are nourished by a pseudo-placenta that transfers nutrients to the enlarged intestine of embryos of *Anableps*, whereas in *Jenynsia* the maternal nutrients are supplied through the mouth and opercular opening of developing embryos.

In the viviparous goodeids, the first several anal fin rays of the male are shorter and offset from the rest of the anal fin by a notch. This is the structure by which sperm bundles are transferred, but the exact mechanism of transfer is unknown. Gestating embryos absorb nutritional ovarian fluids by means of elaborate outgrowths, called "trophotaeniae," which form around the anal region of the embryo.

Excluding *Rivulus marmoratus*, internal fertilization is known in four egg-laying genera, *Campellolebias*, *Cynopoecilus*, *Epiplatys*, and the monotypic *Tomeurus*. *Campellolebias* and *Cynopoecilus* are seasonal genera in the family Rivulidae. Males of *Campellolebias* have a gonopodium, whereas those of *Cynopoecilus* have a modified anal fin in which the first six anal fin rays are bunched together and have prominent contact organs along the rays in the form of papillae. *Epiplatys* is a genus with nearly 50 species, but only one is known to have internal fertilization, a Sudanese population of *Epiplatys bifasciatus*. *Tomeurus gracilis* is a typical gonopodial poeceliine species, except that it expels its eggs. The mechanism of sperm transfer in *Cynopoecilus* and *Epiplatys bifasciatus* is unknown.

The seasonal fishes lay their eggs in the substrate. Typically, a male defends a territory while mostly hovering over and close to the substrate. A receptive female approaches, angling with her head toward the substrate; the male draws near, sometimes wrapping his anal and dorsal fins around the usually smaller female. The pair dives into the substrate, sometimes disappearing from sight. One or more eggs are released by the female and fertilized by the male. After a characteristic rolling motion designed to bury the eggs, the male and female emerge from the substrate. The eggs enter a resting state. The water in these habitats eventually evaporates, and the adults die or, more likely, are eaten by birds before the water is completely gone. Some of the eggs embryonate and hatch during the next rainy season. Even though the next rainy season may be months or, in a drought, years away, in a home aquarium these eggs may hatch after as little as two to three months of storage in damp peat moss. The spawning of seasonal fish continues through the wet season. The eggs of the seasonal killifishes develop asynchronously in the female, not all at once.

Most nonseasonal killifishes are plant spawners. Males court a passing female and, if she is receptive, the pair move to the vegetation and press their bodies together in a characteristic S shape, their bodies quivering as a single egg is released and fertilized. The eggs are adhesive and stick to the vegetation. Aquarists simulate this habitat by providing a faux plant in the form of a small mop made of acrylic yarn. Aquarists often collect the eggs of these killifishes with their fingers. The egg is tough and easily handled without fear of damage, and it has a long developmental period, 10–14 days. As a result, the young hatch without a yolk sac and are fully capable of swimming and feeding, unlike the young of many other fish groups, which pass through a larval stage.

The species *Rivulus marmoratus* is a self-fertilizing hermaphrodite, unique among vertebrates in that respect. Individuals of the species look like typical female *Rivulus*, but they possess both ovaries and testes, with the ability to fertilize their own eggs before laying them. Essentially they are self-cloning. Two types of males are known. Secondary males are hermaphrodites that have become functional males with the color characteristics of a male *Rivulus*, but they retain a small amount of ovarian tissue. Some populations produce primary males, that is, individuals hatching out as males without ovaries. The populations in the Belize Keys have a high percentage of primary males (25%), and there is some evidence that primary males (and possibly secondary males) mate with the hermaphrodites. This might entail a mechanism whereby the presence of a male prompts suppression of self-fertilization in the hermaphrodites. There are killifishes that spawn in cracks and crevices; typically, these are species found in rocky streams and lakes, the procatopodine genera *Procatopus* and *Lamprichthys tanganicanus*, respectively. Some species, such as *Fundulus catenatus*, lay their eggs over shallow gravel beds. The reproductive biology of many killifishes is not known, even though some of them are fairly common.

Conservation status

Approximately 10% of all cyprinodontiform species—92 in all—are cited in the 2000 Red List of the International Union for Conservation of Nature and Natural Resources (IUCN) in the Extinct (10 species), Extinct in the Wild (5 species), Critically Endangered (18 species), Endangered (20 species), Vulnerable (25 species), Lower Risk/Near Threatened (3 species), and Data Deficient (11 species) categories. The cause of all freshwater fish extinctions and the establishment of the other categories of concern are due solely to the harmful effects of human intervention and not to the events of natural history. Sadly, a species of *Cyprinodon* described in 1993 was given the species name *inmemoriam*, since the species was extinct by the time it was described. The Red List is not a static document, and more species may be expected to appear there.

For instance, although huge tracts of the African rainforests are being cleared, not a single killifish from the affected areas is on the 2000 Red List. This is an extreme example of the category Data Deficient, in this case, no data at all. An undescribed *Nothobranchius* species from the Caprivi Strip of Namibia is the only African species listed as Endangered. All *Nothobranchius* habitats, being seasonal, are capable of being severely affected by human activity, so the absence of other *Nothobranchius* from the 2000 list offers small comfort. Numerous species are listed as Extinct in the Wild. Given the history of failure to keep Extinct in the Wild species, such as the monkey spring pupfish, alive as captive animals, unless they are successfully reintroduced into the wild, the future of such species is bleak.

For species listed in any category the reasons why they were listed are cited. Establishing whether a species is extinct is very difficult because of the nature of extinction. The absence of evidence is not necessarily evidence of absence. The difficulties are acute when the actual distribution of a species is imperfectly known or when its taxonomic limits have not been established or when there has been inadequate sampling. Harrison and Stiassny have reviewed this topic. Another 20 species are listed as regionally endangered by various states in the United States. These statistics need to be put into perspective. The percentage (10%) of the Cyprinodontiformes under threat is among the highest in the Actinopterygii, comparable to the carps, of the order Cypriniformes, with 12% of its 2,660 species appearing on the Red List. Live-bearers and killifishes have colonized marginal habitats easily degraded by human intervention or highly vulnerable to introduced exotic species. In addition, their distributions sometimes are highly localized, as, for example, in a single spring or pond. These factors account for the high level of threat occurring in this group.

Significance to humans

Species in the genera *Orestias* in the Andes and *Anableps* in Central and South America are taken in subsistence fishing by local inhabitants. In the bait fish industry in the United States, fundulids, such as *Fundulus heteroclitus*, and cyprinodontids, such as *Cyprinodon variegatus*, are sold routinely as bait fish. In the case of the latter species this sometimes leads to disastrous consequences for the local fauna when end-of-the-day bait-bucket releases occur. Both killifishes and live-bearers are voraciously larvivorous, thus helping to control mosquito populations and their resulting detrimental effects upon humans. In many areas killifishes and live-bearers represent an important forage item for game fishes. In the Everglades, Florida Bay, and the Keys there is an interesting food chain of great economic significance. The salt marsh mosquito is very abundant in southern Florida. The killifishes and live-bearers feed heavily on mosquito larvae, obtaining the energy necessary to produce many offspring. When the killifishes and live-bearers move into the tidal creeks, they provide abundant forage for tarpon, redfish, and snook, which feature heavily in the economy of southern Florida.

A mosquitofish (*Gambusia affinis*) about to feed on mosquitoes. (Photo by Robert Noonan/Photo Researchers, Inc. Reproduced by permission.)

Aquarium hobbyists keep many species of Cyprinodontiformes. Various live-bearers, selectively bred for color and fancy fins, are sold in large numbers. Many specialty hobbyist groups, such as the American Killifish Association, the Deutsche Killifisch Gemeinschaft, the American Livebearer Association, and the Association France Vivipare, have been formed to keep and study these fishes. The cooperation of hobbyists and ichthyologists has had a significant impact on the furtherance of our knowledge of the Cyprinodontiformes. Cyprinodontiform species have been used widely in evolutionary studies, the study of life history patterns, the study of the effects of exotic introductions, and the disciplines of ecology, reproductive biology, genetics, physiology, toxicology, and behavioral psychology. This list is by no means exhaustive. *Xiphophorus hellerii*, *Fundulus heteroclitus*, and *Rivulus marmoratus* alone have accounted for hundreds of articles in professional journals and other publications. The beauty of many of these fishes has led to their being featured on the postage stamps of several countries, which aids in stimulating an interest in conservation efforts.

1. Largescale foureyes (*Anableps anableps*); 2. Redtail splitfin (*Xenotoca eiseni*); 3. Ascotan Mountain killifish (*Orestias ascotanensis*); 4. Northern mummichog (*Fundulus heteroclitus macrolepidotus*); 5. Blackfin pearl killifish (*Austrolebias nigripinnis*); 6. Mangrove rivulus (*Rivulus marmoratus*); 7. Tanganyika pearl lampeye (*Lamprichthys tanganicanus*); 8. Devils Hole pupfish (*Cyprinodon diabolis*); 9. Chocolate lyretail (*Aphyosemion australe*); 10. Green swordtail (*Xiphophorus hellerii* ssp. *hellerii*). (Illustration by Emily Damstra)

Species accounts

Largescale foureyes
Anableps anableps

FAMILY
Anablepidae

TAXONOMY
Anableps anableps Linnaeus, 1758, India (misreported type locality).

OTHER COMMON NAMES
English: Striped foureyed fish, foureyed fish, foureye; Spanish: Cuatro ojos; Portuguese: Quatro-olhos.

PHYSICAL CHARACTERISTICS
Grows to 12 in (30 cm) in total length. Elongate, compressed posteriorly, and flat anteriorly. Blunt snout and toothy horizontal mouth with only a slight curvature. Large, bulging, froglike eyes set far forward, almost on the snout, and divided by a black horizontal band into an upper and lower portion for separately viewing above and below the waterline. Dorsal fin set far back, completely behind the anal fin. Three to five blue to violet horizontal lines of varying lengths run along the sides. Dorsal surface is brownish. A whitish line runs along the back; at the operculum the line divides into a Y shape, each arm of which terminates at an eye. The ventral area is whitish. Sexually dimorphic. Females are larger than males, with rounded fins; males have a tubular, scaled gonopodium.

DISTRIBUTION
Trinidad, Venezuela, Guyana, Suriname, French Guiana, and the Amazon Delta in Brazil.

HABITAT
Found in freshwater, brackish, and saltwater rivers, streams, and estuaries and oceanic saltwater near beaches.

BEHAVIOR
A gregarious schooling fish, sometimes gathering in the hundreds with congeners of equal size. Since they swim with the upper half of their eyes above the water, they have the amusing habit of bobbing their heads up and down so as to keep their eyes wet. This species has been seen riding the breakers near sandy beaches, sometimes getting tossed onto the beach by the waves. Undaunted, foureyes just jumps back in. Because of their acute vision above the water, they are very difficult to capture.

FEEDING ECOLOGY AND DIET
In brackish and marine environments, scores of these fish jump out of the water at low tides to gulp down the mud, which is rich in algae, diatoms, dinoflagellates, amphipods, isopods, and worms. Although they are primarily surface feeders, they leap from the water in pursuit of low-flying insects. Small fishes also are part of their diet, but these fish are not bottom feeders. Not surprisingly, aquarists report that the species will not take food that falls to the bottom of an aquarium.

REPRODUCTIVE BIOLOGY
Foureyes are live-bearers with internal fertilization and matrotrophic (type 2) gestation and development. The male gonopodium swings out in a horizontal plane, but only in one direction, either to the left or to the right. The vent of the female is covered by a hinged scale called a "foricula," which opens to the left or right. Thus, right-handed males must mate with left-handed females and vice versa, an odd situation that does not seem to impede their reproduction. The gestation period is about 20 weeks, with a brood size of 10 to 20 fry. The young are large, up to 2 in (5 cm) at birth. This large size is remarkable, considering that sexual maturity is reached at about 3.5 in (9 cm).

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
All species are taken for food in subsistence fishing, and, to a limited extent, they are sold in the aquarium trade. ◆

Chocolate lyretail
Aphyosemion australe

FAMILY
Aplocheilidae

TAXONOMY
Aphyosemion australe Rachow, 1921, Port-Gentil (formerly Cape Lopez), Gabon.

OTHER COMMON NAMES
English: Chocolate australe, australe, Cape Lopez lyretail, lyretail panchax.

PHYSICAL CHARACTERISTICS
Grows to 2–2.4 in (5–6 cm). Sexually dimorphic and dichromatic. The male is slender-bodied and cylindrical in shape; the body has a slight curve to the dorsal surface. The head tapers to a terminal mouth, and the caudal peduncle is compressed and tapering. Dorsal fin is small and set far back, with its origin over the midpoint of the anal fin. Dorsal surface is chocolate brown, and anterior flanks are light metallic blue; red spots and splotches are scattered over the body and on the dorsal and anal fins. All fins show color, the dorsal and anal fins with orange and red margins. Anal fin tapers to a point, with its color grading into white; the upper and lower parts of the caudal fin have curved white extensions, giving this fin its characteristic lyre-tailed shape. The female is smaller, usually without much color. Sometimes golden, gray, or muddy, with rounded fins and iridescent bluish white margins on the pectoral fins. Body and unpaired fins have tiny red dots. All color and color patterns vary widely for both males and females.

DISTRIBUTION
South along the coasts of Gabon starting at the Ogowe River, the Congo, the Cabinda Enclave (Angola), and Zaire.

HABITAT
Found in swamps associated with small streams and rivers, rainforest swamps, and shallow flooded areas—quiet, weed-choked environments.

BEHAVIOR
A peaceful species, easily kept in a heavily planted aquarium or one provided with spawning mops or with a combination of plants and mops.

FEEDING ECOLOGY AND DIET
Aquarists feed the chocolate lyretail brine shrimp—frozen or live—adult or newly hatched, and such live foods as fruit flies, daphnia, and tubificid worms. In nature, it is assumed that aquatic invertebrates and terrestrial insects are the chief component of the diet.

REPRODUCTIVE BIOLOGY
A typical plant spawner, the male courts the female with fins flared. A receptive female moves to the plants or spawning mop, where the pair presses against each other in an S shape, both of them quivering. The female releases an egg, which the male fertilizes. The adhesive egg sticks to the vegetation or mop. These eggs are collected easily and hatch in 14 days. It is estimated that some aquarium populations of the chocolate lyretail have been held and bred in aquaria continuously since 1913, yet differences are small compared with the wild forms from the type locality.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sold and exchanged among aquarium hobbyists and occasionally available in the aquarium trade. ◆

Devils Hole pupfish
Cyprinodon diabolis

FAMILY
Cyprinodontidae

TAXONOMY
Cyprinodon diabolis Wales, 1930, Devils Hole, Ash Meadows, Nevada, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
A dwarf species seldom exceeding 1 in (2.6 cm) in length. Pelvic fins are absent. Resembles the juvenile pupfish. Sexually dimorphic and dichromatic. Males have iridescent blue body color; the operculum is iridescent with a purple sheen. The unpaired fins are bordered in black, the dorsal fin is iridescent gold, and the anal and caudal fins are whitish toward the base. Prominent genital papilla. Females overall have more yellowish coloration than males. The back and caudal and pectoral fins are yellowish brown, and the dorsal fin is edged in black. The operculum is metallic green, with a hint of a dark bar on the caudal peduncle.

DISTRIBUTION
Ash Meadows, Nevada.

HABITAT
The enclosed pool of an aquifer formed by flooded limestone caverns and reached by a 49 ft (15 m) naturally occurring shaft in the side of a hill, its only source of light. The dimensions of the entire pool are 11.5 ft by 72 ft (3.5 m by 22 m). A boulder divides the surface of the pool into two sections. The breeding and most of the feeding, upon which the survival of the species depends, take place on an algae-covered rocky shelf 11.5 ft by 16.6 ft (3.5 m by 5 m) with 1 ft (0.3 m) of water above it. The shelf is situated at the foot of the shaft. The overall dimensions of this part of the pool are 11.5 ft by 42 ft (3.5 m by 13 m). At the end of the shelf there is an abrupt drop-off of 28 ft (8.5 m). The substrate continues to slope downward below that depth. Water flows in and out of the pool at a year-round temperature of 90°F (32°C). As the lakes and waters of the area disappeared and the desert formed, the species was trapped in the aquifer 10,000 to 25,000 years ago.

BEHAVIOR
The pupfish exhibits a daily cycle of movement to and from the rocky shelf, depending on the time of day and the time of year.

FEEDING ECOLOGY AND DIET
In the summer and fall the species feeds chiefly on the algae growing on the shelf. Algae also grow on the substrate just off the shelf up to a depth of 50 ft (15 m), with only trace amounts below that. In winter and spring, when the algae are much reduced, diatoms are the chief food items. The population varies from about 200 to 500 individuals, depending on the algae growth.

REPRODUCTIVE BIOLOGY
Males do not set up breeding territories, as do other pupfish. Spawning takes place primarily in April and May. Males closely accompany a ripe female to the algae-covered shelf, where they stay together and spawn at irregular time intervals spanning about one hour. The species has spawned in the laboratory, but no eggs were hatched.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
The pupfish has endured in its tiny habitat for as many as 25,000 years, providing us with a stimulus to ponder both the durability and the vicarious nature of life. ◆

Ascotan Mountain killifish
Orestias ascotanensis

FAMILY
Cyprinodontidae

TAXONOMY
Orestias ascotanensis Parenti, 1984, Salar de Ascotan, Chile.

OTHER COMMON NAMES
English: Lake Ascotan Mountain killifish

PHYSICAL CHARACTERISTICS
Grows to 2.4 in (6 cm) in length. A member of the *Orestias agassizii* species complex. Basically olive-green in color, with anal and dorsal fins set back and over each other. The lower jaw turns up. Males and females are robust, with a relatively large head compared with the heads of other species in the species complex. Sexually dimorphic and dichromatic. Males are smaller than females and more slender. Breeding males have a bright yellow overlay on the sides and the anal and dorsal fins. Females are larger and more rounded than males. The fins and body are mottled, tending toward more uniform coloration when they are very mature.

DISTRIBUTION
Known only from Salar de Ascotan, a small saline lake in northwestern Chile, the southernmost population of *Orestias*.

HABITAT
The species is found in the slightly brackish water of Lake Ascotan and its associated ponds, where *Ruppia filifolia* is the most common vegetation.

BEHAVIOR
In 1995, for the purpose of studying captive breeding, Jara, Soto, and Palma set up four males and four females in a planted 3 gallon (12 L) aquarium with no reported aggression among the males. The males did not persistently court the females, as happens with many other killifishes; some time was spent apart, feeding and moving about the aquarium.

FEEDING ECOLOGY AND DIET
In aquaria the species readily feeds on insect larva, crustaceans, and commercial flake food, indicating that in the wild it is a benthopelagic feeder on aquatic invertebrates.

REPRODUCTIVE BIOLOGY
This species is a typical plant spawner. At the lake, eggs were found attached to the vegetation. In aquaria the male courts the female by approaching from beneath and nudging her pelvic area. The two then move to the vegetation. With the pair positioned side by side with their vents close together, the male assumes a typical S-shape posture. The female releases two or three adhesive eggs, which are fertilized by the male. The filamentous eggs adhere to the vegetation. The incubation time is about 17 days at 63–68°F (17–20°C).

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Northern mummichog
Fundulus heteroclitus macrolepidotus

FAMILY
Fundulidae

TAXONOMY
Fundulus heteroclitus macrolepidotus Walbaum, 1792, northern America. In the 1980s, Able and Felley recognized the subspecies status of the northern populations of *Fundulus heteroclitus*.

OTHER COMMON NAMES
English: Killie, killifish; Spanish: Fúndulo; Portuguese: Fundulo.

PHYSICAL CHARACTERISTICS
Grows to 5 in (13 cm) in length. Sexually dimorphic and dichromatic. Males and females have up to 15 vertical bars, which tend to be faint or missing in mature adults. The mouth is blunt, with a turned-up lower jaw. The dorsal fin is positioned over the anal fin origin at about the midbody. Males have a dorsal ocellus. Breeding males are light gray to very black in background color. The body and all unpaired fins have bright iridescent white to greenish opalescent spots. The dorsal, anal, and caudal fins have a yellow margin that is less noticeable on the caudal fin in the black body variety. There is a yellowish cast to the abdomen and operculum, the latter with iridescent silver highlights. Color patterns and color intensities vary widely in both sexes. Females are larger than males. Body is chunky with a pale silvery background, brownish color on the back, and whitish color on the abdomen. The fins are clear. Adults rarely are confused with other species in their natural range.

DISTRIBUTION
From Chesapeake Bay, Maryland, United States, to Newfoundland, Canada. Naturalized in the estuary of the Guadalquivir River, southwestern Spain, and possibly established in the salt marshes of the estuary of the Guadiana River, at Castro Marim, southeastern Portugal.

HABITAT
The species is active primarily in tidally influenced coastal salt marshes as well as estuaries, tidal streams and creeks, shallow marine and brackish environments, and back-beach lagoons reached by high tides. They have been reported for freshwater portions of the Bronx River and naturalized in freshwater impoundments, the latter likely due to bait-bucket releases. Most studies of its habitat use have been undertaken in its primary habitat, the salt marshes.

BEHAVIOR
Traveling in huge schools numbering in the hundreds, the mummichog is in constant search of food. As a result, fishers find that they are caught easily in baited minnow traps. As a predator on salt marsh invertebrates and small fish, and as a prey item for wading birds and the blue crab, the northern mummichog has a significant impact on salt marsh trophic dynamics. The annual mortality rate is about 50% for adults and more than 99% for the larval and juvenile class sizes.

FEEDING ECOLOGY AND DIET
Feeds on a variety of marine and freshwater invertebrates, diatoms, mollusks, amphipods, crustaceans, plant material, insects, detritus, worms, and small fishes. It is doubtful that a mummichog would spurn anything edible that fits into its mouth. Mummichogs are preyed upon by larger fish and fish-eating birds.

REPRODUCTIVE BIOLOGY
Judging by its reproductive behavior in aquaria, the mummichog probably spawns continually in the spring and summer, but in nature its peak spawning activity is governed by a lunar cycle. Eggs are laid in clumps on floating algae mats or at the base of marsh grasses and buried in the sand in the high marshes at the very high tides of the new moon or full moon. The eggs are placed where desiccation will be minimized when the tide goes out. The eggs hatch when they are immersed again at the next very high tide. In aquaria water-incubated eggs hatch in about 16 days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The mummichog is used as a bait fish and as an aquarium animal; it also is one of the most widely used laboratory animals. It is a harmless species unless it is swallowed live. It has been reported that many bored fishers have swallowed live mummichogs. In one such instance, some of the fish were infected with the larva of the nematode *Eustrongyloides ignotus*, causing stomach and intestinal problems for three fishers, two of whom required surgical intervention. Raasch noted, "Though 12 fishermen reported no symptoms from this pastime, the moral is that fishermen should abstain from taking the bait themselves when the fish refuse to do so." ◆

Redtail splitfin
Xenotoca eiseni

FAMILY
Goodeidae

TAXONOMY
Xenotoca eiseni Rutter, 1896, near Tepic, Nayarit, Mexico.

OTHER COMMON NAMES
Spanish: Mexcalpique cola roja.

PHYSICAL CHARACTERISTICS
Males grow to 2.4 in (6 cm) in length and females to 2.8–3 in (7–8 cm). Sexually dimorphic and dichromatic. All fins are rounded. The dorsal fin of males is larger than that of females and is set over the anal fin, far back on the portion of the body that tapers to the caudal peduncle. The body is block-shaped, with a humpbacked appearance in mature fish. The depth of the caudle peduncle is much smaller than the body depth. The head is small and pointed. The basic background color of the body is brownish gray to beige; the degree of dark pigmentation is quite variable. Males are bright orange to red at the base of the caudal peduncle, with iridescent blue highlights on the forward part of peduncle between the anal and dorsal fins. The middle portion of the body has gold highlights, and the abdomen is reddish to yellowish near the operculum. The dorsal fin is sometimes black, the caudal fin is orange to yellow, and the anal fin is orange. Color patterns and intensities vary greatly by location, with colors in alpha males very pronounced. Females have a grayish beige body color, sometimes with silvery highlights; all fins are slightly yellow.

DISTRIBUTION
Mexico in Rio San Leonel, El Sacristan, and Rio Grande de Santiago drainages in Nayarit; also in Rio Tamazula, Jalisco.

HABITAT
Found in rivers, streams, and springs as well as in ditches, which are sometimes highly polluted.

BEHAVIOR
Collects in groups that have an alpha male. Males constantly pursue females and are pugnacious and scrappy toward each other and especially toward other species. In aquaria they have the reputation of being fin nippers.

FEEDING ECOLOGY AND DIET
Omnivorous.

REPRODUCTIVE BIOLOGY
A live-bearing species with internal fertilization, the embryos being nourished by trophotaeniae. The gestation period is about 60 days. Brood size ranges from 10 to 40 fry, with reports of up to 100 fry.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The redtail splitfin is sold in the aquarium trade and is bred and traded by live-bearer aquarium hobbyists. ◆

Tanganyika pearl lampeye
Lamprichthys tanganicanus

FAMILY
Poeciliidae

TAXONOMY
Lamprichthys tanganicanus Boulenger, 1898, Mbiti Rocks, southernmost Lake Tanganyika.

OTHER COMMON NAMES
English: Lake Tanganyika lampeye, Tanganyika pearl killifish, Tanganyika killifish.

PHYSICAL CHARACTERISTICS
Grows to 6 in (15 cm) in length. Sexually dimorphic and dichromatic. Males and females are silvery, sleek, and compressed and taper to the terminal mouth and caudal peduncle. Brightly reflective eyes. They have high-set pectoral fins and dorsal fins set far back, with the origin approximately over the middle of the anal fin. Caudal fins have scales at the base. Recurved teeth noticeable on the outer surface of the upper and lower jaws. Males have an anal fin with a broad base; the rays are shorter than in females. Eight or nine lines of very bright iridescent blue spots along the body, with yellowish spotting on dorsal, anal, and caudal fins and yellow pelvic fins. All observed colors and patterns vary widely, depending on the angle of the lighting. Female are smaller than males, with rounded fins. Shorter dorsal and anal fin base, anal fin rays longer than in the male. The body is silvery or bluish, and the fins are faintly yellow or orange.

DISTRIBUTION
Endemic to Lake Tanganyika.

HABITAT
Rocky shores (not sandy areas) out to a depth of about 30 ft (10 m).

BEHAVIOR
A benthopelagic fish moving in large schools with conspecifics and sometimes in schools of native freshwater herrings. Despite its predilection for schooling, individuals wander about apart from schools. Males are not aggressive toward each other. Fry form huge schools in the hundreds and even in the thousands. In aquaria newly hatched fry form schools at the water surface immediately upon hatching. Fry must be reared apart from the adults.

FEEDING ECOLOGY AND DIET
Feeds on aquatic and terrestrial insects, such as chironomid larvae, termites, and beetles, as well as small crustaceans, ostracods, fish scales, and small fish. The elements of this diet indicate

feeding from the bottom to the surface of the water column. The recurved teeth on the outer surface of the upper and lower jaws facilitate the capture of chironomid larvae and ostracods on rocky substrates. Fish scales and small fishes indicate midwater feeding, while terrestrial insects suggest surface feeding. Aquatic vegetation does not seem to play a part in the diet.

REPRODUCTIVE BIOLOGY
A bottom spawner, utilizing cracks and crevasses for its egg-deposition sites. A male and female meeting in midwater descend to the rocky substrate. The female positions herself close to a crack or crevasse in the rocks, where she ejects an egg, which is fertilized by the male. The eggs are not adhesive but become wedged in place. In aquaria they make use of a similar arrangement of rocky crevasses but also lay their eggs in spawning mops and even on the bare bottom of the aquarium. The eggs are large, 0.1 in (3 mm), but difficult to see. Eggs eye-up in about a week and hatch in two to three weeks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally appears in the aquarium trade. ◆

Green swordtail
Xiphophorus hellerii

FAMILY
Poeciliidae

TAXONOMY
Xiphophorus hellerii Heckel, 1848, Orizaba, Mexico.

OTHER COMMON NAMES
English: Swordtail; Spanish: Cola de espada.

PHYSICAL CHARACTERISTICS
Males grow to 5.5 in (14 cm) in total length, with a sword length of 1.6–3 in (4–8 cm). Females grow to 6.3 in (16 cm). Sexually dimorphic. Males and females have basically the same grayish green background color. Males have a gonopodium, a slender body, a long extension on the bottom of the caudal fin forming a "sword," two lines of reddish dots on a squared-off dorsal fin, and a pronounced line of color that is bright to dark red to almost brown running longitudinally along the body from the snout through the eye to the base of the caudal fin. Sometimes paralleled on the flanks by one or two fainter reddish lines above and below. The sword is an iridescent yellowish green bordered in black. Females are robust and rounded, with squared-off anal and dorsal fins. Caudal fin is asymmetrically rounded, with a hint of a protrusion from the lower part of the fin. There is a shadow on the area over the vent (gravid spot).

DISTRIBUTION
Native distribution in Rio Nantla, Veracruz, Mexico, to northwestern Honduras. Naturalized in the continental United States (ten states) and Hawaii; Michoacan, Morelos, Nuevo Leon, and Coahuila, Mexico; Transvaal, South Africa; Sri Lanka; New Caledonia, Australia; Fiji; Guam; Réunion; and Madagascar.

HABITAT
Inhabit rivers, streams, warm springs and their runoffs, canals, and ponds with heavy vegetation.

BEHAVIOR
While they are not territorial, male swordtails form hierarchical groups. A dominant male drives off rivals within a feeding domain or an area where females have congregated. The mating success rate of a dominant male is about 80% within his area of activity. Females form hierarchical groups of several individuals that stay in close proximity to a dominant male.

FEEDING ECOLOGY AND DIET
Plant material and insects form the greatest part of the diet. In aquaria they are voracious, consuming a wide variety of foods, such as fruit flies, frozen or live brine shrimp and chironomid larvae, flake foods, high-protein paste foods, small fish, and algae.

REPRODUCTIVE BIOLOGY
Green swordtails are live-bearers. Males impregnate females by means of a gonopodium. Females can store sperm and may produce, from a single mating, several broods over an eight-month period. Swordtails undergo lecithotrophic (type 1) gestation and development, with fry being produced approximately every 30 days. Brood sizes are fairly large; 100 or more fry may be produced by a large female.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The green swordtail has considerable economic importance in the aquarium trade and frequently is used in genetic and behavioral research. ◆

Blackfin pearl killifish
Austrolebias nigripinnis

FAMILY
Rivulidae

TAXONOMY
Austrolebias nigripinnis Regan, 1912, La Plata, Argentina.

OTHER COMMON NAMES
Vernacular: Nigripinnis.

PHYSICAL CHARACTERISTICS
A small species, 2–2.75 in (5–7 cm) and rarely more than 2 in (5 cm) long. Relatively deep-bodied and sexually dimorphic and dichromatic. Males are larger than females. All fins are blue-black with an iridescent greenish overlay on the pectorals. Fins are rounded, with relatively large anal and dorsal fin bases. Iridescent metallic-green margin on the dorsal fin and similar margins on the anal and caudal fins are made up of a series of separate spots. Opalescent whitish to greenish spots on all fins and the body, forming five to 11 vertical bars. Lines paralleling the fin edges on the unpaired fins. Body color is sometimes pale around the abdomen. All intensities and patterns vary widely. The female has smaller rounded fins and brown mottling on the body, dorsal fin, and anal fin. Clear caudal, ventral, and pectoral fins and whitish abdominal area.

DISTRIBUTION
The La Plata River basin in Uruguay and Argentina.

HABITAT
Inhabit temporary waters, such as flooded meadows, shallow ponds, and roadside ditches.

BEHAVIOR
The male takes over an area, which it defends against other males. A female moves in, signaling her receptivity by tilting toward the substrate. The male joins the female, and they move side by side with their heads together. The pair spawns directly on the substrate or, conditions permitting, by diving into it. In an aquarium with more than one male, a dominant male, obvious by his black body and fins, defends a spawning area of his choice; the color of the other males fades to light gray, with some black or brownish blotching. If the aquarium is heavily planted so that the males cannot see each other, more than one dominant male may appear.

FEEDING ECOLOGY AND DIET
The species feeds on live foods, such as aquatic and terrestrial insects, worms, crustaceans, and other aquatic invertebrates. In aquaria live foods (such as fruit flies, brine shrimp, chironomid larvae, tubificid worms, and daphnia) are accepted eagerly and almost everything else is rejected, with the exception of chopped earthworms and certain paste foods.

REPRODUCTIVE BIOLOGY
Eggs placed in the substrate during spawning go into diapause. When the temporary waters evaporate, the adults die off, but the eggs survive until they hatch in the next rainy season, within hours of being wetted. Aquarists simulate this environment by providing garden peat moss as the substrate, periodically collecting the peat and storing it away in an almost dry state at a temperature of about 70°F (20°C). When the peat is flooded after two to four months of storage, most of the eggs will hatch. If the eggs do not hatch, the peat can be dried again and flooded at a later date.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The blackfin pearl killifish is exchanged among aquarium hobbyists but only rarely becomes available in the aquarium trade. ◆

Mangrove rivulus
Rivulus marmoratus

FAMILY
Rivulidae

TAXONOMY
Rivulus marmoratus Poey, 1880, "from Cuba, if they do not exist in the United States." Poey's description of the type locality has to be one of the strangest in the history of taxonomy. As it turns out, this species is found in Florida and Cuba; the types are presumed to be from Cuba, Poey's homeland.

OTHER COMMON NAMES
English: Rivulus.

PHYSICAL CHARACTERISTICS
Grows to 3 in (75 mm) in length. Hermaphrodites. Cylindrical in shape, with tapering of the head and caudal peduncle and a high scale count. Dorsal and anal fins are set far back (typical for all *Rivulus* species), with the dorsal fin origin set back farther than the anal fin origin. A characteristic splotchy brown pattern, with an irregular dark mark just behind the operculum (humeral blotch) and a rivulus spot (ocellus) on the caudal peduncle. Primary and secondary males have the same body shape, an orange or pink overlay (more often orange) on the body and fins, mottling, and a dark humeral blotch. The rivulus spot sometimes is absent, unpaired fins at times are clear and at times have dark edges. The proportion of primary males in Belize is high (25%), whereas elsewhere the proportion is very low for both primary and secondary males.

DISTRIBUTION
Florida, Mexico, Belize, Nicaragua, Guatemala, Honduras, French Guiana, Venezuela, Brazil as far south as Santos, the Bahamas, and numerous Caribbean locations.

HABITAT
A semiterrestrial species that inhabits coastal mangrove forests in very shallow water or the wet areas of their muddy flats, out of water under detritus and leaf litter, or under or inside rotting logs. Frequently occurs in the burrows of land crabs. Found in marine and brackish water or in hypersaline pools but not in freshwater.

BEHAVIOR
Can be caught in traps set in crab holes but dies if the traps become flooded, possibly indicating that respiration of atmospheric air is a necessity. They also can be caught on a tiny hook baited with a small piece of worm. Captive individuals jump out of the water to snatch a termite or ant held above the water surface. In nature they flip along the water surface one or more times or leave the water altogether to elude danger. Extremely aggressive toward each other in aquaria, yet small aggregations have been caught in crab burrows and under rotting logs.

FEEDING ECOLOGY AND DIET
Feeds on small terrestrial and aquatic insects, mosquito larvae, polychaete worms, mollusks, and gastropods. It leaves the water to seize food items but returns to the water to eat them.

REPRODUCTIVE BIOLOGY
The only known self-fertilizing vertebrate. Although they are highly efficient at self-fertilization, hermaphrodites release some unfertilized eggs. There is evidence that outcrossing takes place, which would seem to indicate that the hermaphrodites can suppress self-fertilization so that males can fertilize the unfertilized eggs released by the hermaphrodites.

CONSERVATION STATUS
Not listed by the IUCN. Regionally are listed as a species of Special Concern in Florida.

SIGNIFICANCE TO HUMANS
Widely used in field and laboratory studies in genetics, toxicology, ecology, and physiology. ◆

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Organizations

American Killifish Association. 280 Cold Springs Drive, Manchester, PA 17345-1243 USA. Web site: <http://www.aka.org>

American Livebearer Association. 5 Zerbe Street, Cressona, PA 17929-1513 USA. Phone: (570) 385-0573. Fax: (570) 385-2781. Web site: <http://livebearers.org>

Desert Fishes Council. 315 East Medlock Drive, Phoenix, AZ 85012 USA. Phone: (602) 274-5544. Web site: <http://www.desertfishes.org/>

Kenneth J. Lazara, PhD

Stephanoberyciformes
(Whalefishes and relatives)

Class Actinopterygii
Order Stephanoberyciformes
Number of families 9

Illustration: Hairyfish (*Mirapinna esau*). (Illustration by Brian Cressman)

Evolution and systematics

The order Stephanoberyciformes comprises deepwater, bathypelagic fishes that are for the most part poorly known anatomically. The order has a checkered systematic history; some of the families currently assigned to this order were treated as part of the formerly larger order Beryciformes (sometimes called Trachichthyiformes), others were previously included in the Lampridiformes. Stephanoberyciforms, as presently constituted, were given the status of an order by G. D. Johnson and C. Patterson in a phylogenetic survey of acanthomorph teleosts in 1993 (which is followed here); parts of the group were previously recognized as separate orders by earlier authors, including the whalefishes (Cetomimiformes) and pricklefishes and allies (Xenoberyces in part, or Stephanoberyciformes *sensu stricto*).

The 9 families that form the Stephanoberyciformes are divided into 28 genera and about 92 species. The families are:

- Stephanoberycidae (pricklefishes; 3 monotypic genera)
- Melamphaidae (bigscales or ridgeheads; 5 genera, about 38 species)
- Gibberichthyidae (gibberfishes, *Gibberichthys*; 2 species)
- Hispidoberycidae (*Hispidoberyx ambagiosus*)
- Cetomimidae (flabby whalefishes; 9 genera, about 35 species)
- Barbourisiidae (*Barbourisia rufa*)
- Rondeletiidae (redmouth whalefishes, *Rondeletia*; 2 species)
- Mirapinnidae (3 genera, 5 species)
- Megalomycteridae (largenoses; 4 genera, 5 species)

The first four families form the superfamily Stephanoberycoidea; the remaining families are united in the Cetomimoidea. Stephanoberyciforms share a specialization of the posterior dermal skull roof, in which the enlarged extrascapular bones cover the parietal bones. They are closely related to the bony fish groups Zeiformes, Beryciformes (*sensu stricto*), and Percomorpha, sharing with them the presence of pelvic fin spines (lost in certain stephanoberyciforms), as well as specialized features of their pelvic fin anatomy.

The fossil history of the Stephanoberyciformes is almost negligible in contrast to the more extensive fossil history of the Beryciformes. No fossil stephanoberyciform taxon has been erected to date, even though fossil otoliths (paired ear stones of the membranous inner ear labyrinth present in many fishes that can aid in detecting motion) and scant skeletal remains have been mentioned. Otoliths are difficult to identify because they lack features that are diagnostic of taxa of fishes; nonetheless, two unnamed species referred to the living genus *Melamphaes* have been recorded from the Tertiary period (some 50 million years ago) of France.

Physical characteristics

Stephanoberyciforms are a morphologically diverse lineage, ranging from the large-headed whalefishes to the small-headed megalomycterids and mirapinnids. In stephanoberyciforms generally, the head is somewhat large, with numerous bony ridges in the stephanoberycoids (giving them a highly armored look), usually with small eyes, the dorsal and anal fins end in opposition posteriorly on the body, the pectoral fins are of moderate size, and the caudal fin is truncated and not very large. All families have a single dorsal

fin, either with very few spines (stephanoberycoids) or lacking them completely. Pelvic fins can be well developed (as in melamphaids), reduced (as in stephanoberycids), absent (as in cetomimids), and even winglike and aberrant (as in the hairyfish, *Mirapinna esau*). The caudal fin may have procurrent spines (as in stephanoberycoids), and is uniquely subdivided in *Mirapinna*. The jaw bones are rather weak and easily bent.

Many stephanoberyciform species appear velvety due to small protrusions from the epidermis (as in *Mirapinna*), or even from numerous spines on the scales (as in stephanoberycids) that are usually deciduous. Many species, such as the cetomimids, lack scales, others, such as the melamphaids, have large cycloid scales (their scales are rarely seen as they are easily lost on capture). The teeth are very small; numerous pores are usually visible on the head and lateral line, and some species may have luminous tissues and highly distensible stomachs, and are soft and flabby (as in whalefishes). One family, the Megalomycteridae, has extremely well-developed olfactory organs and nostrils. Species of the mirapinnid genera *Eutaeniophorus* and *Parataeniophorus*, and those in the family Megalomycteridae are morphologically quite distinct from other stephanoberyciforms.

The fishes of this order are usually small, rarely surpassing 9.8 in (25 cm) in length, and usually below 4.7 in (12 cm); only a few specimens above 13.8 in (35 mm) are known. Coloration is drab, brown, grayish black, or reddish (as in whalefishes). Many stephanoberyciform species are known from very few specimens, and sometimes these represent only a single sex or a juvenile stage; no adult mirapinnid has been collected to date.

Distribution

The fishes of this order are widely distributed throughout all major oceans, but are yet to be recorded from the Mediterranean Sea or from Arctic waters.

Habitat

Stephanoberyciforms are deepsea fishes, generally inhabiting bathypelagic depths down to about 13,123 ft (4,000 m). A few species, especially juvenile forms, have been captured closer to the surface in waters as shallow as 164 ft (50 m), probably an indication of vertical migrations. The only specimen of the hairyfish was captured near the surface. Stephanoberyciforms, especially whalefishes and melamphaids, form an important and very large proportion of fishes in the bathypelagic realm.

Behavior

Stephanoberyciforms undertake vertical migrations from deeper waters into shallower regions.

Feeding ecology and diet

Very little is known concerning the food preferences of stephanoberyciforms, as the stomachs of relatively few individuals have been found to contain food. Copepods and other small crustaceans have been found in the stomachs of a few specimens of different species, but many, including, stephanoberycoids and whalefishes, are probably capable of ingesting larger prey items because of their relatively wide gape. Stephanoberyciforms are probably eaten by larger fishes.

Reproductive biology

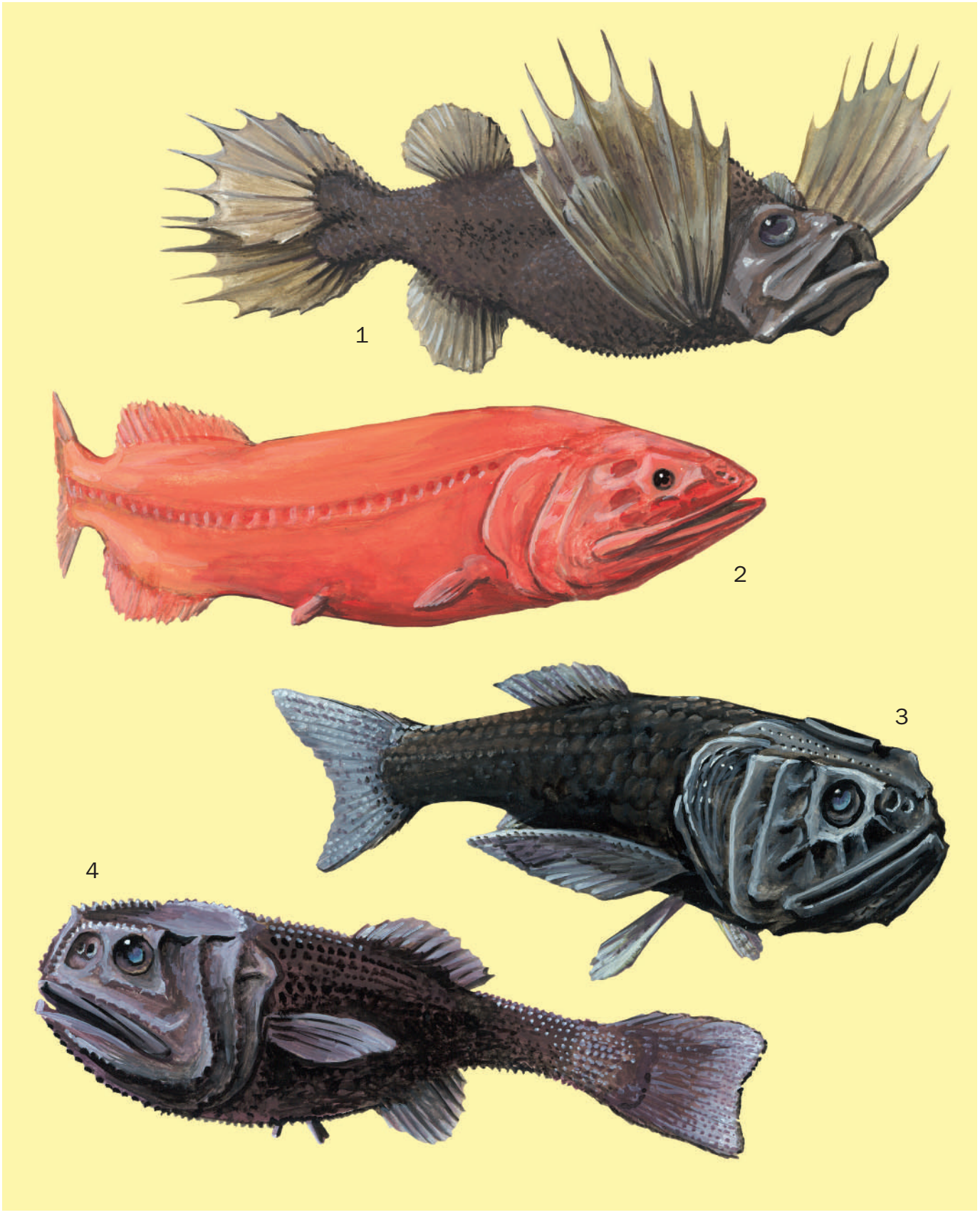
The reproductive biology of stephanoberyciforms is largely unknown, but both eggs and larvae are pelagic. Eggs are unknown in many species. One highly modified larval form was originally described as a separate genus, *Kasidoron*, and even given familial status, but it is now well established that it represents the larval form of the gibberfish (*Gibberichthys pumilus*). This larval form is remarkable, presenting a very long pelvic appendage that superficially resembles algae (such as *Sargassum*) or siphonophores. The appendage is lost by about 1.2 in (3 cm) standard length. The larvae of *Eutaeniophorus* and *Parataeniophorus* are remarkable in presenting very elongated caudal "streamers," long tape-like projections that may reach several times body length (somewhat smaller in *Parataeniophorus*); the streamer is lost in adults. Larvae also have been described for *Melamphaes*, *Poromitra*, *Scopeloberyx*, and *Scopelogadus*. These begin to display their generic characteristics from between 0.2 and 0.8 in (0.5 and 2 cm) standard length. As a general rule, larvae and juveniles appear to occur in more shallow water compared to adults of the same species, which tend to be more bathypelagic.

Conservation status

No species in Stephanoberyciformes are listed by the IUCN.

Significance to humans

Stephanoberyciforms are not eaten and are therefore of little direct importance economically. Whalefishes are very numerous, and believed to form the most numerous fish species in terms of biomass in the bathypelagic zone 3,281–13,123 ft (1,000–4,000 m) in depth; therefore they are probably important food items of other commercial species, such as the orange roughy (*Hoplostethus atlanticus*).



1. Hairyfish (*Mirapinna esau*); 2. Red whalefish (*Barbourisia rufa*); 3. Longjaw bigscale (*Scopeloberyx robustus*); 4. Pricklefish (*Stephanoberyx monae*). (Illustration by Brian Cressman)

Species accounts

Red whalefish
Barbourisia rufa

FAMILY
Barbourisiidae

TAXONOMY
Barbourisia rufa Parr, 1945, Gulf of Mexico.

OTHER COMMON NAMES
English: Velvet whalefish; Japanese: Aka-kujira-uo-damashi.

PHYSICAL CHARACTERISTICS
Length about 15.8 in (40 cm). Unusual, with very large mouth (maxillae extend posteriorly well beyond level of eyes); teeth present on entire length of jaws; single dorsal fin located far posteriorly on back, close to caudal fin, with 20–23 rays; anal fin terminating at same level of dorsal fin, with 14–18 rays; pelvics (with 6 rays) and pectorals (with 12–14 rays) very small; skin covered in minute protuberances (velvety to the touch); lateral line very clearly demarcated by large-pored scales; coloration a uniform bright red.

DISTRIBUTION
Widespread but uncommon, occur in every major ocean usually at low latitudes, but reported to reach as far north as Greenland.

HABITAT
Captured usually near the bottom or in midwater over continental slopes and seamounts in depths of 394–6,562 ft (120–2,000 m).

BEHAVIOR
Benthopelagic, believed to be capable of vertical midwater migrations for feeding.

FEEDING ECOLOGY AND DIET
Nothing known.

REPRODUCTIVE BIOLOGY
Presumably lays pelagic eggs.

CONSERVATION STATUS
Not threatened.

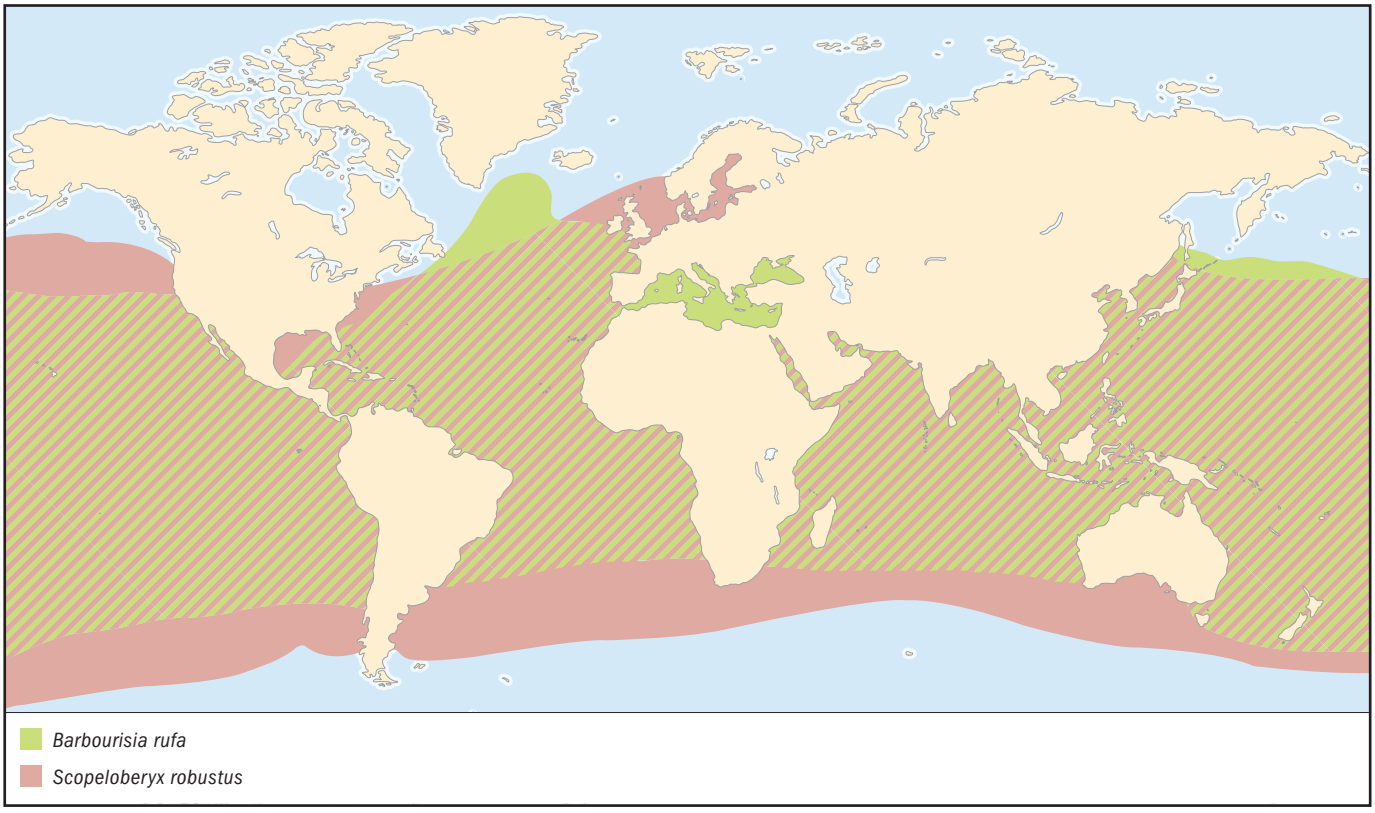
SIGNIFICANCE TO HUMANS
None known. ◆

Longjaw bigscale
Scopeloberyx robustus

FAMILY
Melamphaidae

TAXONOMY
Melamphaes robustus Günther, 1887, Eastern Atlantic.

OTHER COMMON NAMES
English: Ridgehead; Japanese: Tate-kabuto-uo.



PHYSICAL CHARACTERISTICS
Length 2.8–3.9 in (7.3–10 cm). Head large (from 36 to 45% of standard length), with many bony ridges and deep sensory canals; elongate mouth reaching posteriorly well beyond relatively small eyes; large cycloid scales; 19–25 gill rakers; single dorsal fin originating at midlength, with 2–3 spines and 9–13 rays; anal fin posterior to dorsal, with a single spine and 7–9 rays; pelvic fins well posterior to head and with a single spine and 6–8 rays; pectoral fins elongate, reaching to level of middorsal fin, with 11–14 rays; caudal fin with some 20 rays; small teeth in 2–4 rows in upper and lower jaws. Coloration dark brown (at least in preservative).

DISTRIBUTION
Cosmopolitan in all major oceans except the Mediterranean Sea and Arctic Ocean. Reported to be common around the Commander Islands.

HABITAT
Meso- and bathypelagic; adults usually at depths of 1,640–11,102 ft (500–3,384 m), juveniles in slightly shallower waters.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Unknown, but because of its relatively wide gape it may consume fishes.

REPRODUCTIVE BIOLOGY
Probably lays pelagic eggs.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Hairyfish
Mirapinna esau

FAMILY
Mirapinnidae

TAXONOMY
Mirapinna esau Bertelsen and Marshall, 1956, Eastern Atlantic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Size of only specimen 0.16 in (4 cm). Unusual appearance, head region proportionally small; mouth upturned; pelvic fins huge, projecting dorsally and located at throat, with 8 rays; small pectoral fins located more dorsally, with 13 rays; caudal fin divided into 2 distinct lobes that overlap; single dorsal fin posteriorly located, with 16 rays; anal fin opposite dorsal fin, with 14 rays; skin covered in hairlike protuberances; coloration dark brown.

DISTRIBUTION
Known from a single specimen, caught north of the Azores in the Eastern Atlantic.

HABITAT
Only known specimen was caught at the surface.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Copepods were the only food item in the stomach.

REPRODUCTIVE BIOLOGY
Unknown; only known specimen is a juvenile female.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Pricklefish
Stephanoberyx monae

FAMILY
Stephanoberycidae

TAXONOMY
Stephanoberyx monae Gill, 1883, Western North Atlantic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Length 3.9 in (10 cm). Head region proportionally large with many ridges; round eyes; mouth large extending posteriorly beyond level of eyes; single dorsal fin located posteriorly, with 1–3 poorly developed spines and 11–13 rays; anal fin terminating at level of dorsal fin, with 1–3 spines and 11–12 rays; pectoral fins with 12–13 rays; pelvic fins rudimentary and abdominal, with 5

rays; caudal fin with supports over and under caudal peduncle, with 8–11 spines on upper and lower aspects; body covered in scales that have small spines; coloration dark brown.

DISTRIBUTION
Western North Atlantic Ocean, the Caribbean Sea, and the Gulf of Mexico.

HABITAT
Presumably bathypelagic or demersal in relatively deep waters 1,115–15,673 ft (340–4,777 m).

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Unknown, but its large gape suggests it may feed on fishes and invertebrates.

REPRODUCTIVE BIOLOGY
Essentially unknown; two specimens measuring 3 in (8 cm) were sexually mature.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

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Marcelo Carvalho, PhD

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Beryciformes

(Roughies, flashlightfishes, and squirrelfishes)

Class Actinopterygii
Order Beryciformes
Number of families 7

Photo: Four splitfin flashlightfishes (*Anomalops katoptron*), one with its lights off. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The order Beryciformes encompasses 7 marine families, 29 genera, and about 140 species. The seven families are:

- Anomalopidae, the flashlightfishes or lanterneye fishes
- Anoplogasteridae (also spelled Anoplogastridae), the fangtooth fishes
- Berycidae, the alfoncinos and redfishes
- Diretmidae, the spinyfins
- Holocentridae, the squirrelfishes and soldierfishes
- Monocentridae, the pineapplefishes or pineconefishes
- Trachichthyidae, the roughies or slimeheads

The order Beryciformes falls at the base of a large grouping of fishes collectively known as percomorphs. These advanced fishes include the order Perciformes, which comprises a great diversity of fishes including cichlids, perches, blennies, and barracudas. Like all other percomorphs, the beryciforms have a characteristic linked arrangement of the pelvic and pectoral girdles. They differ from other percomorphs in the number of rays in the tail fin. Caudal rays in most percomorphs number 17, but fishes in the Beryciformes order have 18 or 19. Systematists believe that as the fishes advanced evolutionarily, the number of tail-fin rays decreased. The fact that the Beryciformes have a greater number of caudal rays places them at the base of the percomorph lineage.

At one time, the order Beryciformes was larger and included the beardfishes, whalefishes, gibberfishes, and picklefishes. Systematists once classified beardfishes as primitive beryciforms, but have now placed them in their own order, the Polymixiiformes, which precedes the evolution of the Beryciformes. The whalefishes, gibberfishes, and picklefishes are in the order Stephanoberyciformes, and accompany the Beryciformes at the base of the percomorph lineage. The genera of beryciform fishes have also undergone some changes in classification. For example, the squirrelfishes have at one time or another been classified under the genera *Adioryx*, *Flammeo*, *Holocentrus*, *Sargocentron*, and *Neoniphon*, but the latter three are currently used.

The fossil record indicates that beryciform fishes occurred at least as far back as the late Cretaceous period, and were abundant. The group has persisted and is still quite common.

Physical characteristics

The Beryciformes are small- to medium-sized, spiny-rayed fishes, 3–24 in (8–61 cm) long. They have big eyes, some have colorful scales, and some have light organs beneath the eyes. The order is also defined partly by the number of softer, flexible rays in the ventral fin.

Schooling in whitetip soldierfish. (Illustration by Wendy Baker)

The Holocentridae is the largest family within the Beryciformes. Encompassing both the squirrelfishes and soldierfishes, fishes in this family are typified by a reddish color from head to tail and a noticeably forked tail. The trailing edges of their scales often have spines (called spinoid scales); some have spines on their gill covers.

Fishes in the family Anomalopidae, the flashlight or lantern-eye fishes, are distinguished primarily by the obvious light organ under each eye. These fishes and the bioluminescent bacteria that generate the light have developed a symbiotic relationship that offers the bacteria a place to live, while giving the fishes illumination, perhaps for attracting zooplankton during night feeding and for intraspecific communication. Light organs are also seen in other beryciform fishes, including those in the family Monocentridae.

Atlantic flashlightfish (*Kryptophanaron alfredi*) have light organs below their eyes. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

The monocentrids' whimsical common names of the pineapple and pineconefishes come from their beautiful, large scales. Usually yellow, each scale has its own dark outline, further accentuating an armorlike appearance. Like the holocentrids, species of the Monocentridae have spines poking backward from each scale.

Trachichthyids are known mostly from one species, the orange roughy (*Hoplostethus atlanticus*). This somewhat primitive-looking fish, as well as other members of this family, are distinguished by mucous cavities just beneath the skin of the head. This trait accounts for their less-than-flattering alternate common name of slimeheads.

Distribution

As a group, the beryciform fishes are found in tropical, subtropical, and temperate waters nearly around the globe. The

holocentrids occur worldwide in tropical waters, although some venture further north or south. The alfoncinos and redfishes, spinyfins, and fangtooths prefer tropical to temperate waters worldwide. The pineapplefishes share this affinity, but remain in the Indian and Pacific Oceans. The flashlightfishes occur in the tropical seas from the western Atlantic to the Pacific; the roughy family favors the waters around Australia.

Habitat

Beryciform fishes cover a range of habitats. Some species, such as many of the squirrelfishes, gravitate toward shallow, tropical reefs. Others, such as the roughies, spend their lives in deep, dark, ocean waters. Most roughies inhabit continental-shelf and slope waters almost 5,280 ft (1,609 m) deep. Certain spinyfins and fangtooth species share this preference for deep waters, and live along the sea bottom 6,600 ft (2,012 m) down.

Beryciforms that live in shallow waters shun the light, usually tucking themselves under a coral overhang, backing into a cave, or hiding below another structure during the day. During daytime excursions, divers frequently encounter squirrelfishes poking out from some type of dark sanctuary. Shallow-dwelling species sometimes maintain a daily routine of descending into deep waters and remaining mostly inactive during the day, then rising into the shallows at night to feed. A few, such as the flashlightfishes, further avoid the light by limiting their shallow-water forays to nights of a new moon, or to the periods before the moon rises and after it sets.

Behavior

Perhaps the most notable characteristic of the beryciform fishes is their ability to produce light, and in some cases, readily control it. The light is the result of bioluminescent bacteria that take up residence in pockets just below the skin of various species, including the flashlight, pineapple, and pineconefishes. Other beryciform fishes also have light organs, including members in the genera *Sorosichthys* and *Paratrachichthys*. As well as using the light to find and/or to attract prey during their nocturnal feeding forays, in some cases these fishes apparently employ the illumination as a means of communication between members of the their own species and as a method of confusing potential predators. This assumption is based on observations of alterations in the blinking pattern of the light when conspecifics approach one another or when a predator swims nearby. The eyelight fish (*Photoblepharon palpebratus*) can control its light production by lifting or dropping a flap of skin over the light organ. Other species have other ways of controlling the light.

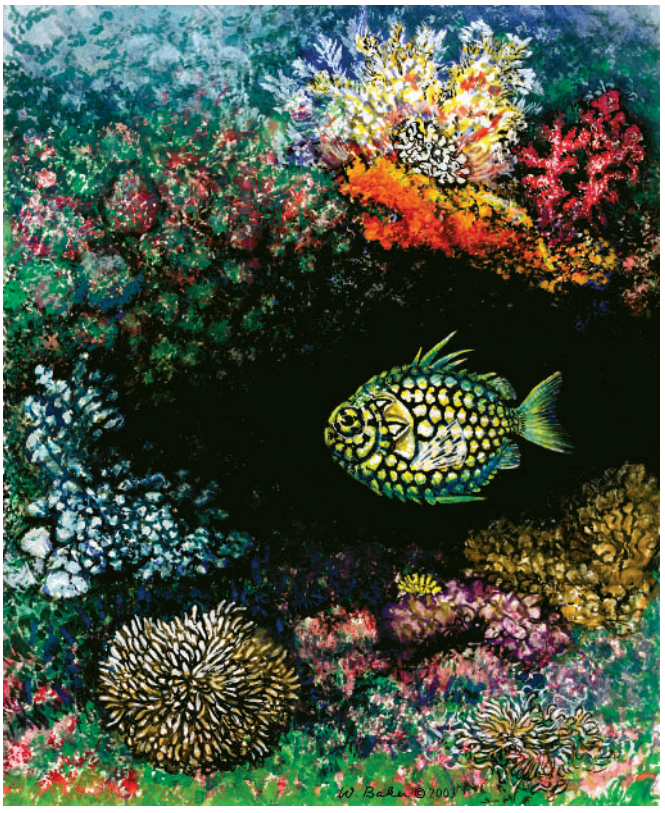
A flashlightfish, with its light organ glowing under its eye in an otherwise dark background. Flashlightfish use the light organ at night to look for prey and to communicate with each other. (Illustration by Wendy Baker)

Hawaiian squirrelfish (*Sargocentron xantherythrum*) in a shipwreck near Hawaii. (Photo by Andrew G. Wood/Photo Researchers, Inc. Reproduced by permission.)

Several beryciform species also make noises, either when interacting with members of their own species or with other fishes. The squirrelfishes are noted for their grunting and clicking sounds, which they produce with the swim bladder.

Feeding ecology and diet

Beryciformes feed on small fishes and various invertebrates. The shallow-dwellers are primarily nocturnal feeders, although some will feed on invertebrates passing through their diurnal retreats. For example, squirrelfishes primarily dine on the small fishes, various crabs, shrimps, and other crustaceans and zooplankton they find in the reef at night, but will take an invertebrate during the day if one happens to wander nearby.



A pineapplefish (*Cleidopus gloriamaris*) hides during the day in a rocky opening. (Illustration by Wendy Baker)

Blotcheye soldierfish (*Myripristus berndti*) school in Hawaii. (Photo by Andrew G. Wood/Photo Researchers, Inc. Reproduced by permission.)

Fishes in this order are known by their large eyes, which allow them to see in low-light conditions. Some have the added advantage of light organs, which assist in finding and perhaps attracting prey. Species in the Monocentridae and Anomalopidae use their light organs to fill their diet of crustaceans. The Australian pineapplefish (*Cleidopus gloriamaris*) has light organs near the mouth and uses them like bluish spotlights at night when it ventures out from its cave hideout to find food. The similar-appearing pineconefish (*Monocentris japonica*) is believed to use its light organs to lure light-responsive prey after it has seen them rather than to find them in the first place.

Predators for these fishes may include sea birds for shallow-dwelling species, as well as many of the larger, piscivorous fishes of their habitat.

Reproductive biology

Little is known about the reproductive biology of the Beryciformes. No observations or studies have shown hermaphroditism or sex reversal among the species; they are born male or female and remain that way throughout their lives. Scientists believe that all beryciform fishes have external fertilization.

More is known about the reproduction in squirrelfishes, because these fishes are common in reefs where they are frequently observed by divers. During mating in the Hawaiian squirrelfish (*Sargocentron xantherythrum*), a male and female grunt and click, align themselves side by side, and place their tails together while fanning out their heads to the left and right.

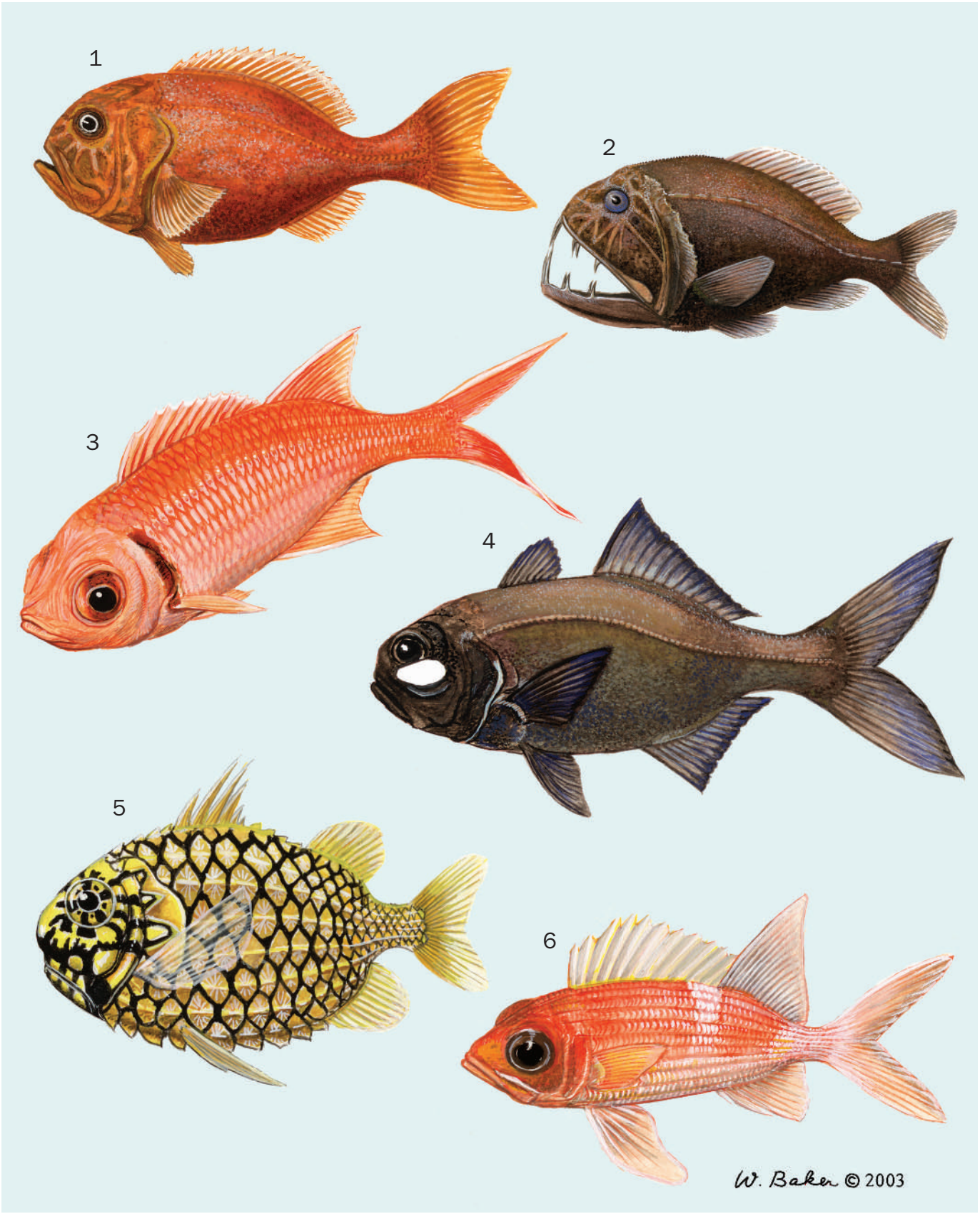
The mating of the red soldierfish (*Myripristis murdjan*) in the Holocentridae, has also been observed. The male and female courtship ritual involves an inward-spiraling swimming pattern between the two, followed by a quick, adjacent rise through the water when both eggs and sperm are ejected for fertilization.

Conservation status

No species of Beryciformes is listed by the IUCN.

Significance to humans

Various members of the Beryciformes are important in the pet trade. The colors of the pineapplefishes and squirrelfishes and the glowing organ of the flashlightfishes all draw interest from aquarium keepers. Divers also appreciate the reds of the shallow-dwelling squirrelfishes, even if they are mostly viewed in dark crevices and other hiding spots during the day. Several beryciforms, including the orange roughy, are commercially harvested as food.



1. Orange roughy (*Hoplostethus atlanticus*); 2. Common fangtooth (*Anoplogaster cornuta*); 3. Blackbar soldierfish (*Myripristis jacobus*); 4. Splitfin flashlightfish (*Anomalops katoptron*); 5. Pineconefish (*Monocentris japonica*); 6. Squirrelfish (*Holocentrus ascensionis*). (Illustration by Wendy Baker)

Species accounts

Splitfin flashlightfish
Anomalops katoptron

FAMILY
Anomalopidae

TAXONOMY
Anomalops katoptron Bleeker, 1856, Manado, Sulawesi [Celebes], Indonesia.

OTHER COMMON NAMES
English: Flashlightfish, great flashlightfish, Indian flashlightfish, lanterneye fish; twofin flashlightfish; German: Lanternenfisch.

PHYSICAL CHARACTERISTICS
Reaches length of nearly 12 in (about 30 cm). The smaller splitfins average about 4 in (10.2 cm) and live in shallower areas. Color brownish black. Has the typical large eye of the beryciforms. They have two dorsal fins; the hindmost fin is triangular and much larger than the front dorsal fin. Two light organs are noticeable just beneath each eye.

DISTRIBUTION
Western South Pacific, from Malaysia east to the Tuamotu Archipelago, and from the Great Barrier Reef up to southern Japan.

HABITAT
Prefers deeper reef areas of 650–1,300 ft (200–400 m), but is also seen in depths as shallow as 65 ft (20 m). During the day, it remains hidden from sunlight, either in deep water or in dark caves. In winter months, the species aggregates in the warmer, shallower waters of the Philippines.

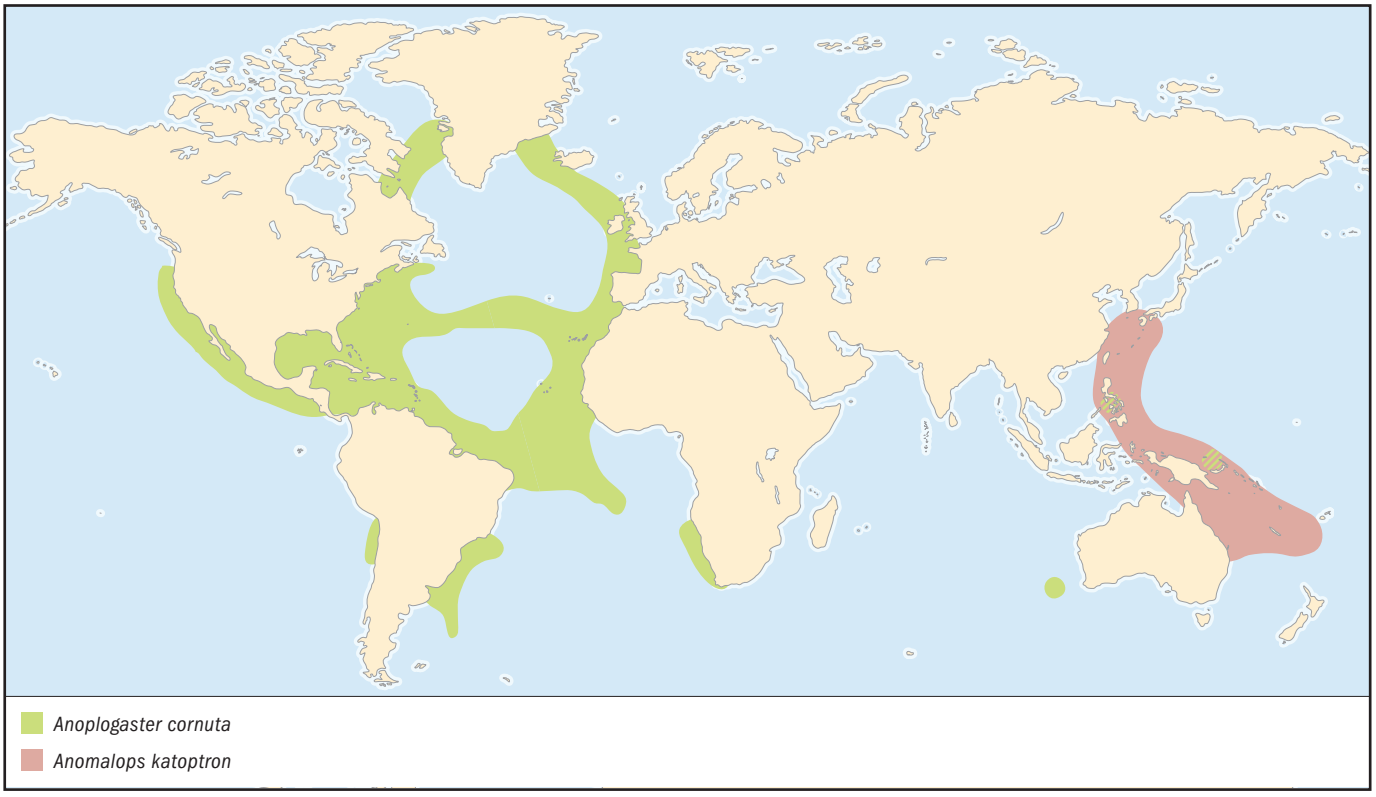
BEHAVIOR
Fishes in this species have a light-producing organ, and regulate it using a muscular attachment that rotates the gland, either to allow the bioluminescent bacteria to shine forth or to hide the glow from view. The fishes can control the light, which they use to communicate with conspecifics. Splitfin flashlightfishes often travel in schools of 24 to 48 fish.

FEEDING ECOLOGY AND DIET
Uses its large light organ during feeding, which is primarily a nocturnal activity. These fishes shun even dim external light, opting to search for food before or after the moon has risen and set, or on nights of a new moon. Their diet is mainly zooplankton.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of the splitfin flashlightfish, but they probably do not guard eggs.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Part of the aquarium trade; sometimes used as bait fish. ◆



Common fangtooth
Anoplogaster cornuta

FAMILY
Anoplogasteridae

TAXONOMY
Anoplogaster cornuta Valenciennes, 1833, S. Atlantic.

OTHER COMMON NAMES
English: Common sabertooth, ogrefish; Spanish: Pez con colmillos.

PHYSICAL CHARACTERISTICS
Can reach up to 6 in (15.2 cm) in length. Their huge head, large mouth opening, and long, sharp teeth combine to give these fishes a rather frightening appearance. With long spines on their heads, the light-gray juveniles look quite different from adults, and were identified as a separate species for many years.

DISTRIBUTION
Temperate to tropical waters around the world.

HABITAT
Prefers deeper waters of 1,650–6,600 ft (500–2,000 m), but some occur as far down as 16,100 ft (4,900 m). Juveniles will venture almost to the surface.

BEHAVIOR
Fangtooths live singly or in small groups.

FEEDING ECOLOGY AND DIET
Adult fangtooths are mainly piscivores, feeding by opening their large mouth to draw in prey. The young primarily subsist on crustaceans.

REPRODUCTIVE BIOLOGY
Engages in external fertilization, and provides no parental care to eggs or young. The larvae are planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Squirrelfish
Holocentrus ascensionis

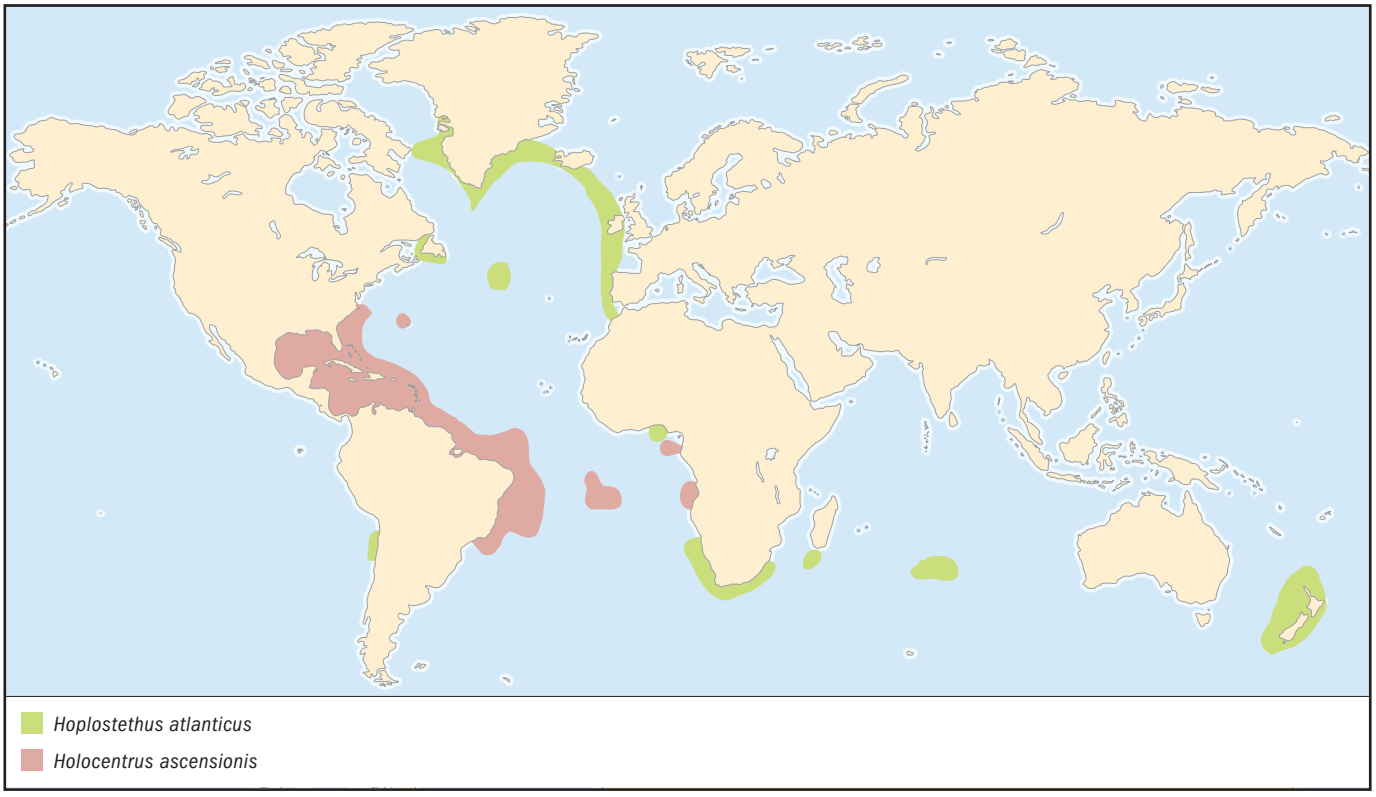
FAMILY
Holocentridae

TAXONOMY
Holocentrus ascensionis Osbeck, 1765, Acension Island.

OTHER COMMON NAMES
English: Common squirrelfish, longjaw squirrelfish, French: Marignan coq; Spanish: Candil gallito.

PHYSICAL CHARACTERISTICS
A reddish, sometimes blotched, fish with a large dark eye. Typically grows to about 12 in (30.5 cm), although reports exist of specimens twice that size. Has a double dorsal fin, with the front fin comprising sharp spines and taking a yellowish hue. The back fin is much taller, with flexible rays.

DISTRIBUTION
Gulf of Mexico and the western Atlantic Ocean from New York to Brazil, and east to Bermuda. Eastern Atlantic in



Gabon, Angola, St. Paul's Rocks, St. Helena, and Ascensión Island.

HABITAT
Subtropical reefs with suitable structures for hiding during the day. Commonly seen by divers in very shallow waters, but also found at depths down to 590 ft (180 m).

BEHAVIOR
Remains hidden from view during the day, either in deeper waters or in shallow-water crevices. May occur alone or in aggregations of up to a few dozen fish. This species makes grunting and clicking noises.

FEEDING ECOLOGY AND DIET
Mainly nocturnal feeders, consuming crustaceans and other invertebrates. Predators include sea birds and other fishes, such as the common dolphinfish (*Corphaena hippurus*), mutton snapper (*Lutjanus analis*), and yellowfin tuna (*Thunnus albacares*).

REPRODUCTIVE BIOLOGY
Mating behavior includes a pairing of male and female, during which they bring their tails together while their heads face away from one another. The eggs are pelagic. The larvae often venture far out to sea, and return to the reefs as adults.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Enjoyed by divers in their natural habitat, squirrelfishes are also part of the aquarium trade. ◆

Blackbar soldierfish
Myripristis jacobus

FAMILY
Holocentridae

TAXONOMY
Myripristis jacobus Cuvier, 1829, Martinique Island, West Indies; Brazil; Havana, Cuba.

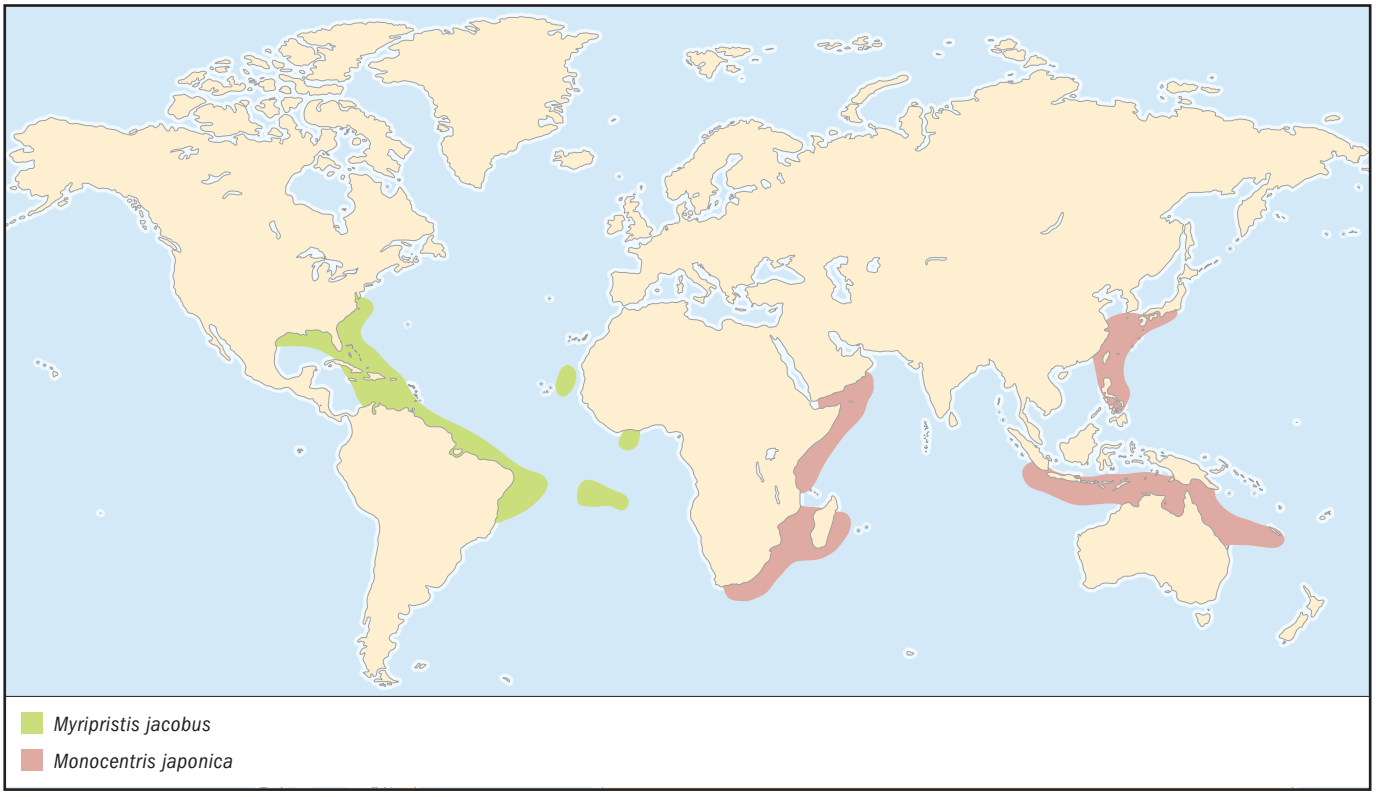
OTHER COMMON NAMES
English: Bastard soldierfish, roundhead conga; French: Marignon mombin; Spanish: Candil de piedra.

PHYSICAL CHARACTERISTICS
Grow up to 10 in (25 cm) in length. Somewhat similar in appearance to the squirrelfish, they are red with a large eye, double dorsal fin, and forked tail, but also sport a brownish black, vertical bar behind the gillcover that extends to the pectoral fin.

DISTRIBUTION
Gulf of Mexico and the eastern Atlantic, north to North Carolina and south to Brazil.

HABITAT
Reefs and other structures, including piers. Commonly seen by divers in very shallow waters, but also found at depths to 330 ft (100 m).

BEHAVIOR
Usually a solitary species, but small groups of up to 36 individuals sometimes school. Under stress, blackbar soldierfishes will make clicking and grunting noises with the swim bladder.



Divers have seen an occasional blackbar soldierfish swimming upside down, and they commonly swim upside down in caves.

FEEDING ECOLOGY AND DIET
Nocturnal feeder. Eats shrimp and zooplankton. Predators include such fishes as the horse-eye jack (*Caranx latus*), West Atlantic trumpetfish (*Aulostomus maculatus*), and Nassau grouper (*Epinephelus striatus*).

REPRODUCTIVE BIOLOGY
Engage in external fertilization on days following a full moon. While the adults prefer shallower reefs, the larvae may travel well out to sea.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Major part of the pet trade and a minor commercial food fish. ◆

Pineconefish
Monocentris japonica

FAMILY
Monocentridae

TAXONOMY
Monocentris japonica Houttuyn, 1782, Nagasaki, Japan.

OTHER COMMON NAMES
English: Dick bridegroom fish, Japanese pineapplefish, knight fish, pine sculpin; French: Poisson ananas; German: Japanischer Reuterfisch/Tannenzapfenfisch.

PHYSICAL CHARACTERISTICS
Can reach 6.5 in (16.5 cm) in length. Has large scales bordered in black. The scales are armed with spines that point toward the tail. The light organ is located near the mouth.

DISTRIBUTION
Southern Japan, spreading down to southern Australia, and west to the Red Sea.

HABITAT
Prefers rocky reefs. The young are found in shallow waters of 10–20 ft (3 to 6.1 m); the adults inhabit depths of 60–700 ft (18–213 m).

BEHAVIOR
Usually solitary or in pairs, but individuals sometimes congregate in schools of 50–100.

FEEDING ECOLOGY AND DIET
Nocturnal feeder. Searches sandy sea bottoms for prey, which includes small fishes, shrimps, and other invertebrates.

REPRODUCTIVE BIOLOGY
Mostly unknown, but they probably do not guard the eggs or young.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Pineconefishes are a minor part of the aquarium trade. ◆

Orange roughy
Hoplostethus atlanticus

FAMILY
Trachichthyidae

TAXONOMY
Hoplostethus atlanticus Collett, 1889, Florés, Azores, sta. 203, 1557 m.

OTHER COMMON NAMES
English: Deep sea perch, red roughy, slimehead; French: Hoplostète orange; German: Degenfisch, Granatbarsch, Kaiserbarsch; Spanish: Raloj anaranjado

PHYSICAL CHARACTERISTICS
Among the largest of the beryciform fishes, and possibly the largest, with some specimens up to 29.5 in (75 cm) in length. Has vivid orange-red coloration and a slightly jutting lower jaw.

DISTRIBUTION
Disjunct populations in tropical, subtropical, and temperate waters worldwide.

HABITAT
Prefers deep waters 590–5,900 ft (180–1,800 m) deep over steep or rough structures, particularly seamounts.

BEHAVIOR
Apparently sedentary rather than migratory. Remains in deep waters most of its life. Little is known about the young, but they are believed to primarily inhabit deep waters, too.

FEEDING ECOLOGY AND DIET
Diet is made up of small fishes, shrimps, squids, and other invertebrates. Predators include other fishes of their habitat, such as basketwork eels (*Diastobranchus* spp.).

REPRODUCTIVE BIOLOGY
Large groups of orange roughies congregate in annual mating schools. The schools may last one to two weeks, during which mature adults (30 years old and more) spawn and then leave the area. Females produce 10,000–90,000 eggs, which are fairly large at 0.08 in (2 mm) and spherical. The eggs drift toward the surface, where they hatch about two weeks later.

CONSERVATION STATUS
Although the orange roughy is not listed by the IUCN, catches have been restricted to help ensure a continued commercial harvest.

SIGNIFICANCE TO HUMANS
Best known as a commercial food fish, providing millions of pounds of harvest each year. Commercial harvests are now restricted, but past annual harvests have topped 100 million pounds (45 million kg) in the waters off Australia and New Zealand. ◆

Resources

Books

Deloach, Ned. *Reef Fish Behavior*. Jacksonville, FL: New World Publications, 1999.

Helfman, Gene S., Bruce B. Collette, and Douglas E. Facey. *The Diversity of Fishes.* Malden, MA.: Blackwell Science, 1997.

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Nelson, Joseph S. *Fishes of the World.* New York: John Wiley Sons, Inc., 1994.

Paxton, John R. "Squirrelfishes and Their Allies." In *Encyclopedia of Fishes.* 2nd edition, edited by John R. Paxton and William N. Eschmeyer. San Diego: Academic Press, 1998.

Snyderman, Marty, and Clay Wiseman. *Guide to Marine Life: Caribbean, Bahamas, Florida*. New York: Aqua Quest Publications, 1996.

Periodicals

Gauldie, R. W., and J. B. Jones. "Stocks, or Geographically Separated Populations of the New Zealand Orange Roughy, *Hoplostethus atlanticus*, in Relation to Parasite Infestation, Growth Rate, and Otolith Shape." *Bulletin of Marine Science* 67, no. 3 (2000): 949–972.

Leslie Ann Mertz, PhD

Zeiformes
(Dories)

Class Actinopterygii
Order Zeiformes
Number of families 6

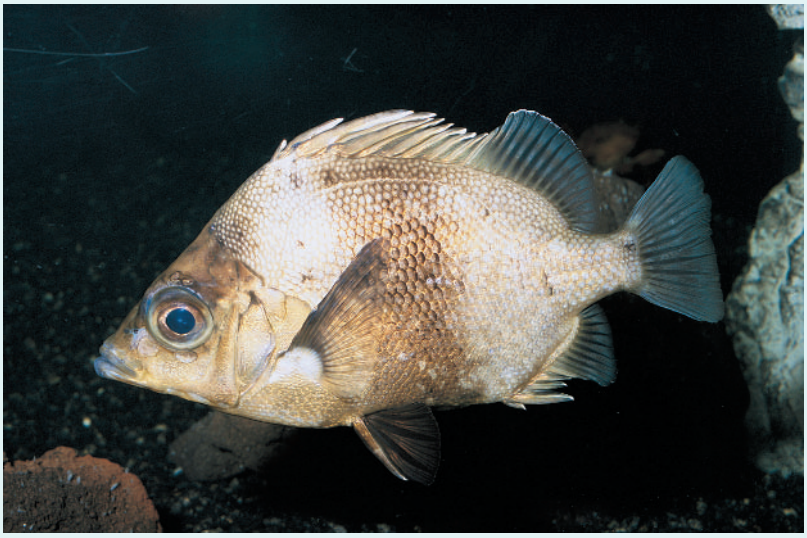


Photo: A Japanese boarfish (*Pentaceros japonicus*) from costal Japan. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Fossils identified as zeiform fishes are confined to marine habitats and are relatively young, ranging in age from Oligocene to Holocene deposits. They have been found in Europe, the West Indies, South Africa, and Indonesia. The phylogenetic relationships of the Zeiformes were explicated by Johnson and Patterson in their 1993 publication on the phylogenetic relationships of the percomorph fishes. They recognized Zeiformes as a monophyletic taxon characterized by the following shared derived characters. There is a distinctive configuration of upright columnar processes on the dorsal elements of the gill arch skeleton. Baudelot's ligament originates immediately under the vagus foramen of the exoccipitals. The distal part of the proximal middle radials of the dorsal fin pterygiophores is expanded laterally. The palatines have a specialized, mobile articulation with the ectopterygoid, which is truncated dorsally. The metapterygoid is extremely reduced, and a continuous median cartilage extends below the frontals and between the ethmoid cartilage and pterosphenoids.

Based on what they term "admittedly tenuous evidence," Johnson and Patterson considered the Zeiformes to be the sister taxon of a group making up the order Beryciformes and a huge conglomeration of spiny-rayed fishes known as the "percomorpha," including the Perciformes, Pleuronectiformes (flounders, soles, etc.), Tetraodontiformes (triggerfishes and pufferfishes, among others), Scorpaeniformes (scorpionfishes, gurnards, flatheads, and so on), Dactylopteriformes (helmet gurnards), Synbranchiformes (swamp eels, spiny eels, and others), Elassomatidae (pygmy sunfish), Gasterosteriformes (pipefish, trumpetfish, etc.), Mugiloidei (mullets), and Atherinomorpha (Atheriniformes, Beloniformes, and Cyprinodontiformes).

The order Zeiformes comprises six families: Zeidae, Parazenidae, Zeniontidae, Oreosomatidae, Grammicolepidae, and Caproidae. In their 1966 seminal paper on the phylogenetic relationships of teleost fishes, P. H. Greenwood and collaborators included the boarfishes (family Caproidae) in the Zeiformes, but they presented no evidence to support this assignment. Heemstra excluded the Caproidae from the Zeiformes in his 1980 taxonomic revision of the zeid fishes of South Africa, and in the book *Smiths' Sea Fishes*, Heemstra included the Caproidae in the order Perciformes. For the purposes of this publication, the Caproidae are included in the Zeiformes.

Much work remains to be done on the systematics of the Zeiformes, and the classification adopted here is tentative. The composition, definitions, and distinction of the families Zeidae, Zeniontidae, and Parazenidae are unsettled. The genus *Cyttomimus* (Gilbert, 1905) appears to be related closely to *Capromimus* (Gill, 1893). Although these two genera seem to be placed correctly in the Zeiformes, their affinity with any of the families recognized here is unclear. The genus *Macrurocyttus* (Fowler, 1933) may belong in the Zeniontidae, but the head of *Macrurocyttus acanthopodus* (Fowler, 1933) looks very different from those of the two species of *Zenion* that are known.

Physical characteristics

The body is deep, compressed, and oblong to disk-shaped. The upper jaw is more or less protrusible, and there are minute, slender, conical teeth in the jaws and vomer. Adults range in size from the dwarf dory (*Zenion hololepis*) at 4 in (10 cm) to the 3-ft (90 cm), 12-lb (5.3 kg) South African Cape dory (*Zeus capensis*). Most species are silvery, bronzy, brown, or reddish. The John Dory is silvery or bronzy, with indistinct longitudinal dark stripes from head to tail and a conspicuous white or yellow-edged black ocellus in the middle of

the body. The juvenile buckler dory (*Zenopsis conchifer*) is silvery and covered with scattered, vaguely defined black spots. Dories can change from silvery to dark brown or gray in seconds. Males and females are colored similarly.

Zeiform fishes can be recognized by the following combination of characters: five to ten dorsal fin spines; zero to four anal fin spines; pelvic fins with one spine and five to seven soft rays or no spine and six to 10 soft rays; a caudal fin with 11, 13, or 15 principal (segmented) rays, of which 9, 11, or 13 rays are branched; and unbranched dorsal, anal, and pectoral fin rays. The orbitosphenoid bone is absent, and there is no subocular shelf or supramaxilla. There are seven or eight branchiostegal rays, 3.5 gills (no slit behind the last hemibranch), 25–46 vertebrae, and a gas bladder.

Distribution

The order is represented in the western Atlantic from Canada to Argentina, including the Gulf of Mexico and the Caribbean Sea. In the eastern Atlantic, zeiforms are known from the North Sea to South Africa, including the Mediterranean, Black Sea, Azores, Madeira, Canary Islands, Cape Verde Islands, and Saint Helena. In the Indian Ocean, zeiforms occur along the east coast of Africa to the Gulf of Aden, Oman, the Persian Gulf, Pakistan, India, Sri Lanka, Maldives, and Madagascar and eastward to the Andaman Sea, Burma, Thailand, Cambodia, Indonesia, Vietnam, Australia, New Zealand, New Guinea, the Philippines, China, Taiwan, Japan, and Korea. In the eastern Pacific, zeiforms range from Canada to Chile.

Habitat

Most zeiform fishes are demersal, living near the bottom of the continental shelf or upper continental slope region. They range in depth from 110 to 5,084 ft (35–1,550 m). The adult John dory (*Zeus faber*), and probably adults of some other zeiform species, frequently occurs in midwater or near the surface. Some species have a pelagic prejuvenile stage that lives near the surface in the open ocean. Adults are found over soft (sandy or muddy) or hard (rocky) substrata.

Behavior

Little is known of the behavior of zeiforms, as they live at depths where they are difficult to observe. Adults of the John dory (*Z. faber*) are mainly solitary. The buckler dory (*Z. conchifer*) often occurs in small aggregations.

Feeding ecology and diet

Zeiform fishes are carnivores; they feed mainly on a variety of fishes but also consume cephalopods and crustaceans. Juveniles of the larger species and adults of the dwarf dories (family Zeniontidae) and tinselfishes (family Grammicolepidae) feed on zooplankton (e.g., copepods, pteropods, fish and crustacean larvae). Adults of the larger zeiform fishes (John dory and the buckler dory) are eaten only by large piscivorous predators (e.g., some sharks, goosefishes [*Lophus* species], and lancetfishes [*Alepisaurus* species]). Juveniles and adults of small zeiforms (e.g., *Zenion* species) are subject to predation by a variety of piscivores.

Reproductive biology

The sexes are separate. Females grow larger than males. Spawning has not been observed, but zeiforms apparently are "broadcast spawners," with the eggs and sperm released into the water column and fertilization taking place in the sea. The eggs and larvae are pelagic and float near the surface; the eggs are spherical, 0.04–0.1 in (1–2.8 mm) in diameter, with a single oil globule. There are no reports of nests or egg guarding or parental care in zeiform fishes.

Conservation status

None of the zeiform fishes are listed by the IUCN. Some populations probably are overexploited in areas where intensive trawling takes place.

Significance to humans

The larger species of zeiforms are of some commercial importance as food fishes. Most zeiforms are caught by trawlers, but anglers also catch a few of the larger species.

1. Buckler dory (*Zenopsis conchifer*); 2. John dory (*Zeus faber*); 3. Red boarfish (*Antigonia rubescens*); 4. Thorny tinselfish (*Grammicolepis brachiusculus*); 5. Tinselfish (*Xenolepidichthys dalgleishi*). (Illustration by John Megahan)

Species accounts

Red boarfish
Antigonia rubescens

FAMILY
Caproidae

TAXONOMY
Antigonia rubescens Günther, 1860, Japan.

OTHER COMMON NAMES
English: Pink boarfish.

PHYSICAL CHARACTERISTICS
Attains a total length (including the tail fin) of about 6 in (15 cm). The head and body are deep, greatly compressed, and shaped like a disk or diamond; the body depth is more than twice the head length. The dorsal head profile and the predorsal region are concave, and there is a bulge on the nape. The body, cheeks, and operculum are covered with small ctenoid scales. The mouth is small, and the upper jaw is shorter than the eye diameter. The dorsal fin has nine spines and 27–30 soft rays; the anal fin has three spines and 24–28 rays. The tail fin has 10 branched rays. The body is pale reddish silvery, with a dark red bar from the dorsal fin origin to the origin of the anal fin; another red bar lies above and below the eye, and there is a red band on the body at the rear of dorsal and anal fin bases. The abdomen and lower rear part of the head are silvery white.

DISTRIBUTION
Japan, Midway Island northwest of Hawaii, Taiwan, Philippines, China, and Australia.

HABITAT
Adults are usually caught with trawls near the bottom at depths of 333–3,000 ft (100–900 m).

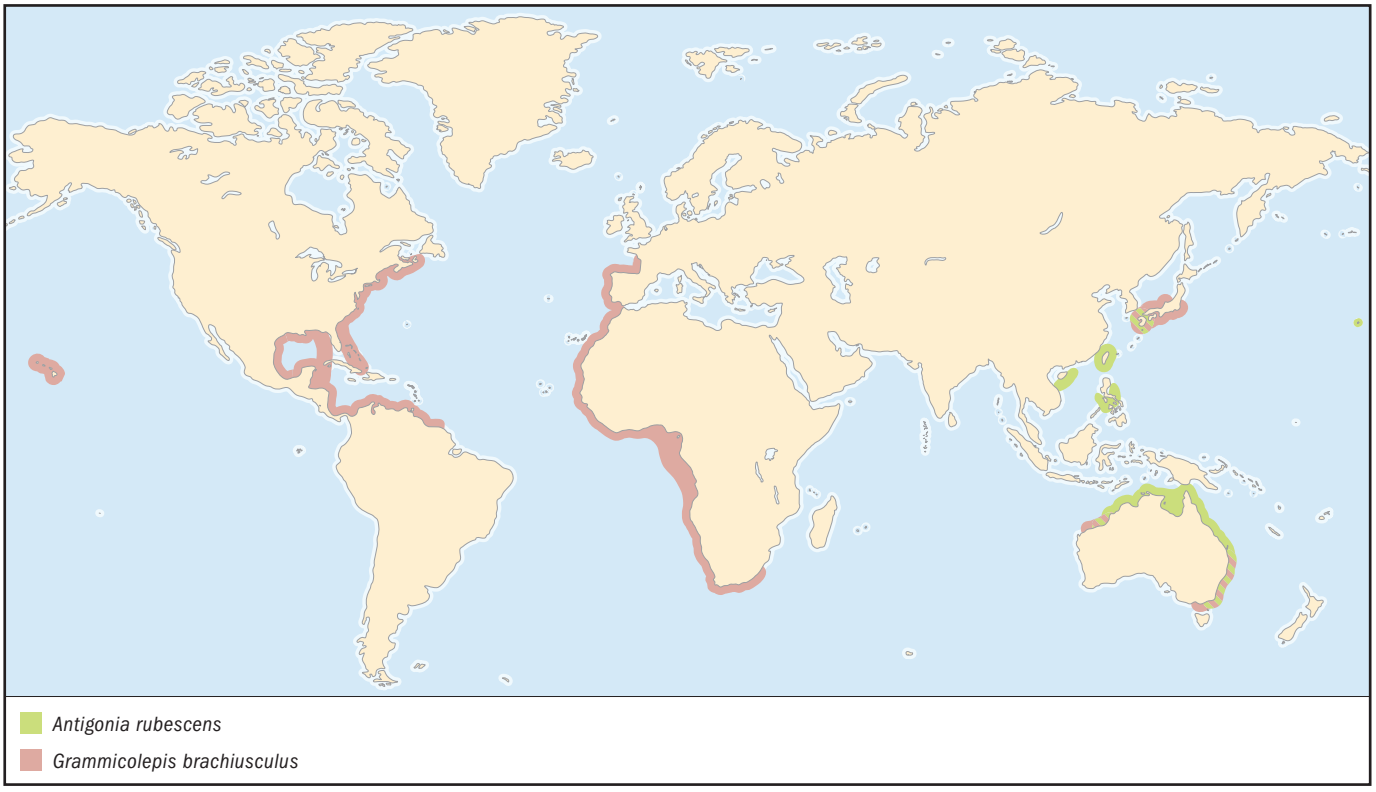
BEHAVIOR
The behavior of the red boarfish is poorly known, because it lives too deep to be observed easily. They occur in large aggregations, as many individuals may be caught in a single trawl haul.

FEEDING ECOLOGY AND DIET
No information has been published on the diet of the red boarfish. Probably feeds on plankton and small benthic invertebrates. Subject to predation by various piscivores that inhabit the outer shelf and slope region (e.g., sharks, lancetfishes, and gempylids).

REPRODUCTIVE BIOLOGY
Poorly known. Probably a broadcast spawner, with pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



Thorny tinselfish
Grammicolepis brachiusculus

FAMILY
Grammicolepidae

TAXONOMY
Grammicolepis brachiusculus Poey, 1873, Cuba.

OTHER COMMON NAMES
English: Diamond dory, deepscale dory; Spanish: Palometa oropel.

PHYSICAL CHARACTERISTICS
Attains a total length (including the tail fin) of about 2 ft, 5 in (72 cm) and a weight of 9 lb (4 kg). The head and body are deep, very compressed, and shaped like an oblong disc, or dinner platter; juveniles are diamond-shaped. The body, cheeks, and operculum are covered with vertically elongated scales. The mouth is small, and the maxilla has two or three ridges, bound to the ascending processes of the premaxillae and loosely connected to the palatines. The jaws have one or two rows of minute, slender teeth, and the vomer may or may not have three or four minute, slender teeth. There are two dorsal fins, the first with six to seven spines and the second with 31–34 unbranched soft rays. The anal fin has two spines and 33–35 unbranched rays. The tail fin has 13 branched rays. The pelvic fins have one spine and six branched rays; there is a row of 34–36 small spines along each side of the dorsal and anal fin bases.

Juveniles have a greatly elongated first anal fin spine and second dorsal fin spine. The pelagic juvenile stage (4–8 in, or 10–20 cm in standard length) looks quite different from the adult. The body is more compressed and angular, with 10–13 prominent, flattened, bladelike, spiny scutes projecting laterally from the surface of each side of the body. Each scute is an outgrowth from a scale whose basal part is divided, overlapping both sides of the one behind. On the base of the larger scutes are retrorse spinules. The scutes become smaller as the fish grows, and they eventually shrink to nothing as the fish transforms to an adult at about 10–12 in (25–30 cm). Adults are silvery in color, with bronze reflections. Juveniles are silvery, with irregular black blotches on the body, black spots on the tail fin, and 5 black bars on anal fin.

DISTRIBUTION
Tropical and temperate waters of the eastern Atlantic from France to South Africa; also known from Japan, Hawaii, Australia, and the western Atlantic from Canada to Suriname.

HABITAT
Adults usually are caught with trawls near the bottom, at depths of 1,333–3,000 ft (400–900 m).

BEHAVIOR
The behavior of the thorny tinselfish is poorly known, as this species has yet to be observed in shallow water.

FEEDING ECOLOGY AND DIET
No information has been published on the diet of the thorny tinselfish. It probably feeds on plankton and small benthic invertebrates. Juveniles are subject to predation by a variety of piscivores. Adults are eaten by some large sharks and lancetfishes.

REPRODUCTIVE BIOLOGY
Poorly known. Probably a broadcast spawner with pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN. Its apparent rarity may be due to the difficulty in sampling fishes from depths of 1,333–3,000 ft (400–900 m).

SIGNIFICANCE TO HUMANS
None known. ◆

Tinselfish
Xenolepidichthys dalgleishi

FAMILY
Grammicolepidae

TAXONOMY
Xenolepidichthys dalgleishi Gilchrist, 1922, Natal, South Africa.

OTHER COMMON NAMES
English: Diamond dory; spotted tinselfish.

PHYSICAL CHARACTERISTICS
Attains a total length (including tail fin) of about 6 in (15 cm). The head and body are greatly compressed and vertically elongated, shaped like a flattened diamond. The body, cheeks, and operculum are covered with vertically elongated scales. The mouth is small and the maxilla, which has two or three ridges, is bound to the ascending processes of the premaxillae and loosely connected to the palatines. The jaws have one or two rows of minute, slender teeth; the vomer has a few minute, slender teeth. There are two dorsal fins, the first with five spines and the second with 27–30 unbranched soft rays. The anal fin has two spines and 27–29 unbranched rays. The tail fin has 13 branched rays, and the pelvic fins have one spine and six branched rays. There is a row of 29 small spines along each side of the dorsal fin and 26–27 small spines along the anal fin base. Juveniles have a greatly elongated (two or three times the length of the fish) first anal fin spine and second dorsal fin spine. The body is silvery with scattered, round black spots; the rear margin of tail fin is dusky.

DISTRIBUTION
Western Atlantic from Canada to southern Brazil and eastern Atlantic from Senegal to South Africa; also in Japan, Taiwan, Philippines, Australia, New Zealand, New Caledonia, Fiji, and Tonga.

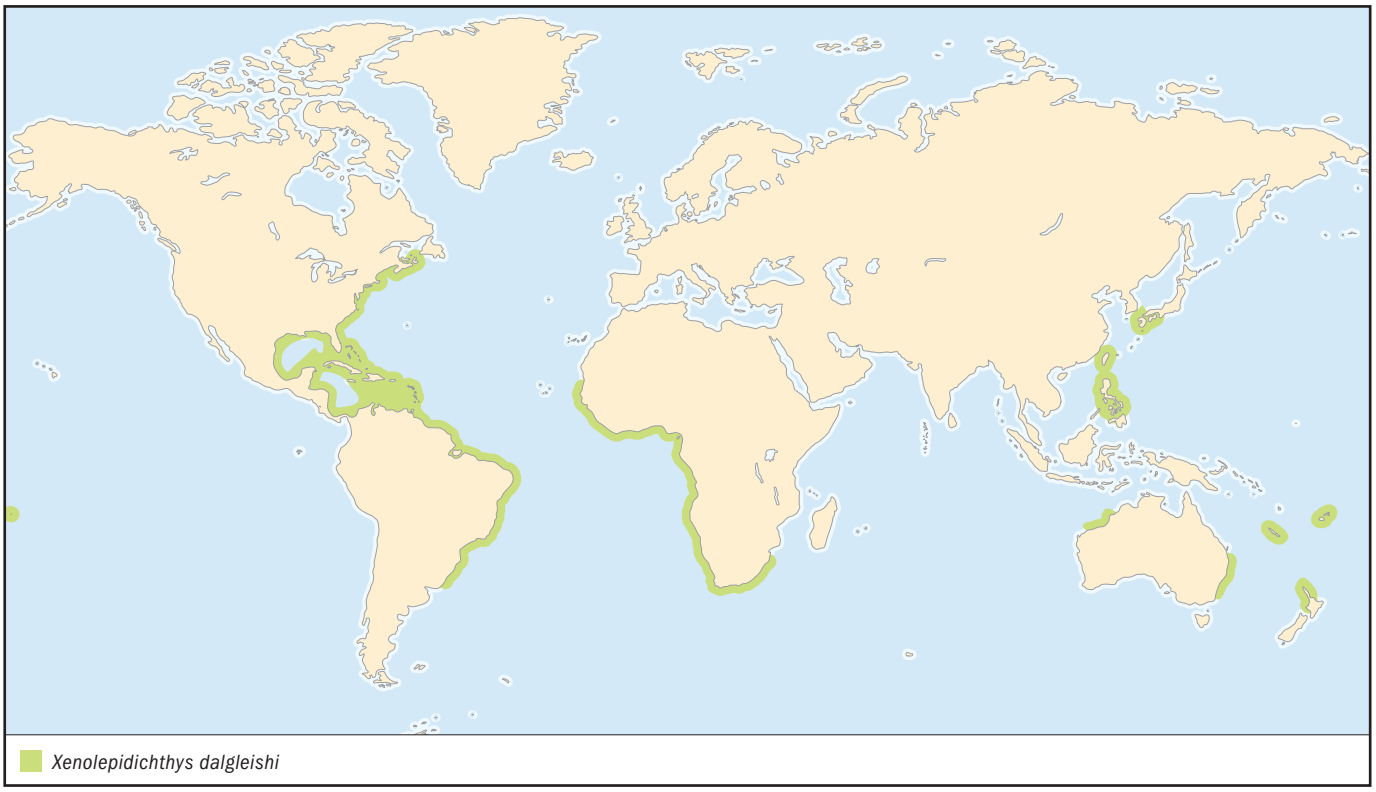
HABITAT
Usually taken near the bottom in depths of 666–1,333 ft (200–400 m) but also taken in midwater and at the surface of the open ocean.

BEHAVIOR
The behavior of the tinselfish is poorly known, as this species is rarely observed in shallow water.

FEEDING ECOLOGY AND DIET
There is no information. Probably feeds on zooplankton and small benthic invertebrates. The tinselfish is prey for some sharks, lancetfishes, scombrids, carangids, and gempylids.

REPRODUCTIVE BIOLOGY
There is no information. Probably a broadcast spawner.

CONSERVATION STATUS
Not listed by IUCN.



SIGNIFICANCE TO HUMANS
None known. ◆

Buckler dory
Zenopsis conchifer

FAMILY
Zeidae

TAXONOMY
Zeus conchifer Lowe, 1852, Madeira.

OTHER COMMON NAMES
English: Mirror dory (Australia), sailfin dory, silvery John Dory; Portuguese: Peixe galo, falo branco.

PHYSICAL CHARACTERISTICS
Attains a total length (including the tail fin) of 2 ft, 8 in (80 cm) and a weight of 9 lb (4 kg). The head and body are very compressed and shaped like an oblong disc, or dinner platter. The dorsal head profile is slightly concave. Dorsal fin spines of the adult are elongated and filamentous. The body has no scales. There is a row of five to eight bony bucklers, each with a strong spine, along each side of the bases of the anal and both dorsal fins. There are two or three bucklers on the isthmus and ventral midline of the chest in front of the pelvic fins and seven or eight pairs of bucklers (ridged bony scutes) along the ventral midline of the abdomen, from the base of the pelvic fins to the first anal fin spine. The thoracic region is compressed. The pelvic fins are large and close together, inserted on the chest below the eyes and well in front of the pectoral fins. Each has six or seven soft rays. The first pelvic ray could be considered a spine, because it is unbranched and not segmented, but (unlike the pelvic fin spine of *Zeus*) it is a biserial (double) ray. There are five to eight bony bucklers (enlarged, platelike scales) along the base of the soft dorsal and anal fins and seven to 10 pairs of spiny scutes along the belly, from the base of the pelvic fins to the anus. The dorsal fin has nine to 10 spines and 24–27 rays; the anal fin has three spines (the first two movable and the third fixed) and 24–26 rays. The caudal fin has 11 branched rays; the pectoral fins are much smaller than the pelvic fins, with 12 or 13 rays. Dorsal, anal, and pectoral fin rays are unbranched. Adults are silvery with a faint, dusky mid-lateral spot above the pectoral fin and below the lateral line. Small juveniles, 1–4 in (2–10 cm) long, are covered with scattered small black spots.

DISTRIBUTION
Mainly continental. Western Atlantic from Canada to Argentina, including the Gulf of Mexico and Caribbean Sea, and eastern Atlantic from France and British Isles to South Africa. Also in the Indian Ocean from South Africa to Kenya and India.

HABITAT
Adults are found over soft (sandy or muddy) or hard (rocky) substrata. They are demersal, usually caught near the bottom of the continental shelf or upper continental slope region at depths of 33–1,188 ft (10–360 m). Occasionally found in midwater well above the bottom.

BEHAVIOR
The behavior of the buckler dory is poorly known, as this species is rarely observed in shallow water. Adults usually are found in aggregations near the bottom. A slow, stalking, ambush-predator mode of hunting is assumed, and the greatly protrusible upper jaw compensates for the feeble swimming musculature.

FEEDING ECOLOGY AND DIET
Feeds on demersal fishes, crustaceans, and cephalopods and often makes excursions above the bottom to feed on midwater fishes. Prey species selection is influenced by availability and accessibility. The dominant species in the diet is likely to be the most abundant prey in the habitat. Adult buckler dory have few predators other than great white sharks and goosefish (*Lophius* spp.). Juveniles are likely prey for most piscivorous predators.

REPRODUCTIVE BIOLOGY
Reproduction is similar to that of the John dory (see following account).

CONSERVATION STATUS
Not listed by IUCN. The species is taken as bycatch in various trawl fisheries in the North Atlantic, off southern Brazil, Namibia, and South Africa. There are no fishing regulations or catch data that apply specifically to the buckler dory.

SIGNIFICANCE TO HUMANS
None known. ◆

John dory
Zeus faber

FAMILY
Zeidae

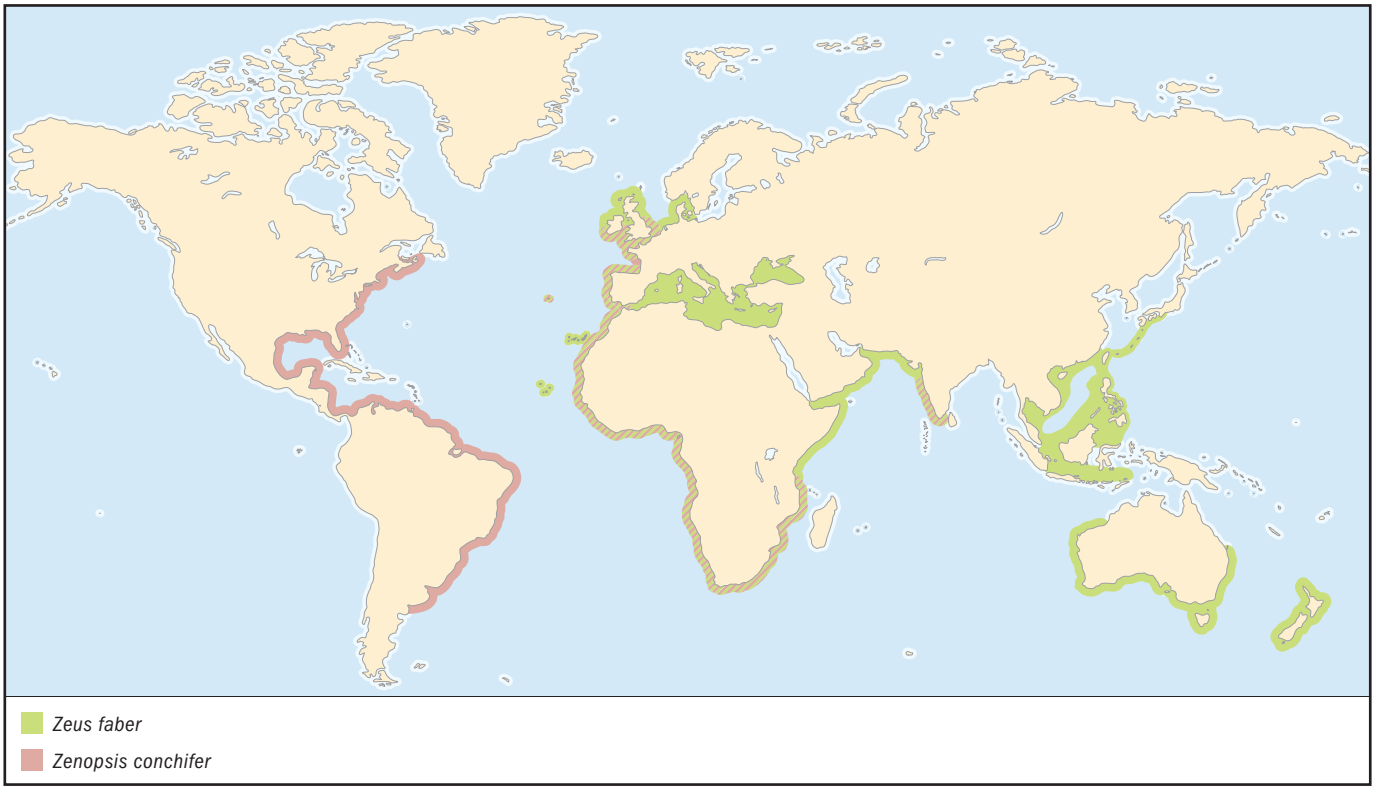
TAXONOMY
Zeus faber Linnaeus, 1758, habitat in Pelago.

OTHER COMMON NAMES
French: Saint-Pierre; German: Heringskönig; Spanish: Pez de San Pedro, gallo de San Pedro, barbero, gallo barbero; Portuguese: Peixe galo.

PHYSICAL CHARACTERISTICS
Attains a total length (including the tail fin) of 3 ft (90 cm) and a weight of 18 lb (8.2 kg). The head and body are very compressed and shaped like an oblong disc, or dinner platter. The dorsal head profile is straight. The dorsal fin spines of the adult are greatly elongated and filamentous. Scales are minute, cycloid, and embedded; there are five to eight bony bucklers (enlarged, platelike scales) along the base of the soft dorsal and anal fins and seven to 10 pairs of spiny scutes along the belly from the base of the pelvic fins to the anus. The dorsal fin has nine to 11 spines and 22–24 rays, and the anal fin has four spines and 20–23 rays. Dorsal, anal, and pectoral fin rays are unbranched, and the caudal fin has 11 branched rays. The pelvic fins are enlarged, situated below and slightly in front of the pectoral fins, with one spine and six or seven branched rays. The pectoral fins are much smaller than the pelvic fins.

The head and body are silvery to olive-brown, with a conspicuous yellow or white-edged, blue-black ocellus on the middle of the body below the lateral line. The body often has indistinct dark, wavy stripes. The dorsal fin spine filaments are white. Juveniles are small, about 1 in (2–3 cm) long. Color is brownish, with small black spots along the base of the median fins, curved white and black stripes on the head and body, and the usual round black spot on the middle of the body below the lateral line.

DISTRIBUTION
Eastern Atlantic from the North Sea to South Africa, including the Mediterranean Sea, Black Sea, Azores, Madeira, and Ca-



nary and Cape Verde Islands and along the west coast of Africa to Namibia. In the western Indian Ocean from South Africa to Somalia and India. In the western Pacific in Indonesia, the Philippines, China, Taiwan, Japan, Australia, and New Zealand. Not known from the eastern Pacific or western Atlantic.

HABITAT

Adults are found over soft (sandy or muddy) or hard (rocky) substrata; they are demersal, usually caught near the bottom of the continental shelf or upper continental slope region at depths of 33–1,188 ft (10–360 m). Adults also frequently occur in midwater or near the surface.

BEHAVIOR

Adults usually are solitary, although they probably congregate for spawning. They typically occur near the bottom, but they often make excursions above the bottom to feed on midwater fishes. With its greatly compressed head and body, large mouth, and extremely protrusible upper jaw, the John Dory is a successful ambush predator. It slowly approaches an unsuspecting small fish by means of undulating waves of the transparent soft dorsal and anal fins. In one quick motion it drops the "trapdoor" lower jaw, shoots out the upper jaw, and expands the gill cavity, sucking in the hapless prey along with a considerable volume of water.

FEEDING ECOLOGY AND DIET

The John dory is a carnivore, feeding primarily on fishes, crustaceans, and cephalopods. Prey species selection is influenced by the availability and accessibility of prey. The dominant species in the diet is likely to be the most abundant prey in the habitat. In the North Atlantic, juveniles, 3–10 in (8–25 cm), feed mainly on benthic fishes, for example, dragonets (family Callionymidae) and Norway pout (family Gadidae). Adults, 10–22 in (25–56 cm), switch to a diet of larger schooling fishes, primarily blue whiting, *Micromesistius poutassou* (Risso, 1826), and snipefish, *Macroramphosus scolopax* (Linnaeus, 1758), of the family Macroramphosidae. Adults have few predators, except for great white sharks and goosefishes (*Lophius* spp.). Juveniles are probably eaten by piscivorous predators.

REPRODUCTIVE BIOLOGY

The John dory is a broadcast spawner. The eggs and sperm are shed simultaneously into the water, where fertilization takes place. In the northeastern Atlantic, spawning occurs in April or May. The eggs and larvae are pelagic; the eggs are small (0.1 in or 2 mm diameter) and spherical, with a large oil globule. No nest building or parental care has been reported for the species. In the North Atlantic, John dory males mature in their second or third year at a length of about 10 in (26 cm), and they may live to an age of 13 years. Females are three or four years old when they become mature at a length of 14 in (35 cm). They grow larger than males do, and they may live 15 years. In New Zealand waters males attain maturity at 11.8 in (30 cm) in two years; their growth then slows considerably, with a maximum size of about 15.7 in (40 cm) and an age of nine years. Females grow faster and attain a maximum size of about 18.1 in (46 cm) and an age of nine years.

CONSERVATION STATUS

Not listed by IUCN. As of 1998 there were no regulations regarding John dory fishery in the English Channel or in Australian waters. The species is taken as bycatch in the trawl fisheries of the eastern Atlantic, South Africa, Australia, New Zealand, Indonesia, Philippines, Taiwan, and Japan.

SIGNIFICANCE TO HUMANS

The John dory is prized as a food fish and is of commercial importance because of its high price in fish markets. ◆

Resources

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Phillip C. Heemstra, PhD

Gasterosteiformes

(Sticklebacks, seahorses, and relatives)

Class Actinopterygii
Order Gasterosteiformes
Number of families 11

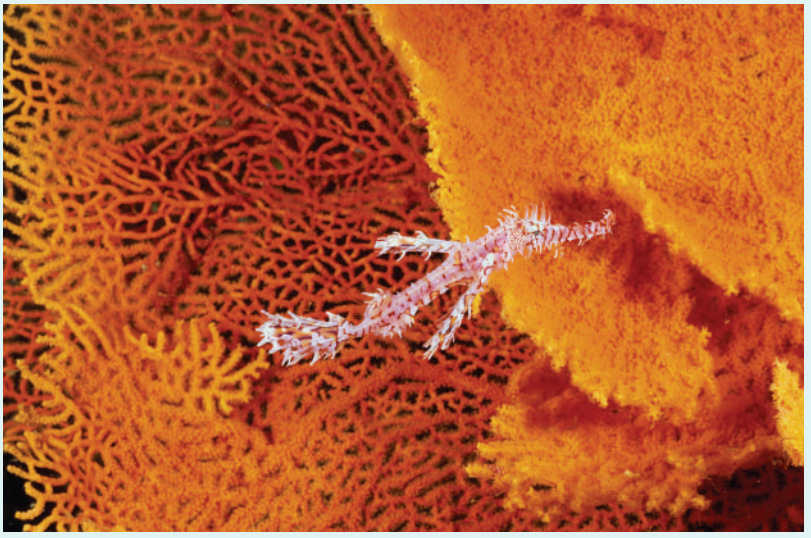


Photo: The ornate, or harlequin, ghost pipefish (*Solenostomus paradoxus*) is a well-disguised seahorse relative that is rarely seen due to its highly effective camouflage. Here it is swimming by a sea fan. (Photo by Robert Yin/Corbis. Reproduced by permission.)

Evolution and systematics

The evolutionary affinities and composition of the Gasterosteiformes have been the subject of much debate; presently they are considered to be closely related to the teleost fish orders Synbranchiformes (swamp eels), Elassomatiformes (pygmy sunfish, *Elassoma*), Mugiliformes (mullets), and the collective Atherinomorpha (silversides, needlefishes, killifishes, and allies) and are placed with them in the larger group Smegmamorpha. Smegmamorphs are characterized by a unique configuration of the first vertebra and its associated intermuscular bone. Within this group, gasterosteiforms may be more closely related to the Synbranchiformes, but relationships within smegmamorphs are still the subject of controversy. The smegmamorphs, in turn, are closely related to the largest of all teleost groups, the Percomorpha. This evolutionary arrangement is the most recent and best-supported hypothesis based on morphological evidence, but alternative schemes of relationship have been proposed (including molecular studies), and a true consensus has not yet emerged.

The Gasterosteiformes, as described in this chapter, comprises two suborders, the Gasterosteoidei and the Syngnathoidei. Other authors sometimes have recognized these as separate orders, but evidence exists that they are each other's closest relative and therefore warrant being classified together. Gasterosteiformes share various specializations, such as pelvic bones without anterior processes, absence of Baudelot's ligament (a stout ligament connecting the shoulder girdle to either the posterior cranial base or an anterior vertebra—also absent in synbranchiforms), certain features of their branchial and caudal skeletons, and a particular configuration of their scales, which are represented by enlarged scutes, or plates. (Scales are absent in *Hypoptychus*, *Aulostomus* has small ctenoid scales, and *Fistularia* has embedded spines). The extent to which these features (and others) are truly indicative of a common ancestry for Gasterosteiformes is not completely understood.

The Gasterosteoidei includes the following families: Hypoptychidae (for the sand eel, *Hypoptychus dybowskii*), Aulorhynchidae (tubesnouts, two monotypic genera), Indostomidae (*Indostomus*, with three species), and Gasterosteidae (some five genera and, conservatively, seven spp.). The Syngnathoidei comprises the families Syngnathidae (seahorses and pipefishes, with about 52 genera and 220 spp.), Aulostomidae (trumpetfishes, *Aulostomus*, with some three spp.), Fistulariidae (cornetfishes, *Fistularia*, with four spp.), Macroramphosidae (snipefishes, three genera with 12 spp.), Centriscidae (shrimpfishes, two genera with four spp.), Solenostomidae (ghost pipefishes, *Solenostomus*, with some four spp.), and Pegasidae (seamoths, two genera with five spp.). Altogether, the order Gasterosteiformes is represented by 11 families, 70 genera, and at least 265 species, but undescribed species have been discovered (including some 20 species of pipefishes and seahorses), and numerous nominal species presently in synonymy, in fact, may be valid (such as for sticklebacks). Much work remains to be done concerning their taxonomy, and the phylogenetic position of *Indostomus* is still debated.

The fossil record of the Gasterosteiformes is extensive and dates back at least some 75 million years to the Calcare di Mellissano deposits near Nardò, in southeastern Italy (Apulia). This early fossil, *Gasterorhamphosus zuppichinii*, is known from skeletal remains and is similar to modern snipefishes. Additional gasterosteiform fossils, known from more or less complete skeletons, have been described from the extensive Monte Bolca beds of northeastern Italy (dating back some 52 million years). These include representatives of the Syngnathidae (at least five genera), Solenostomidae (some three

Breeding habits of the yellow seahorse (*Hippocampus kuda*): 1. Prenuptial courtship—male on right; 2. Nuptial embrace—female ejects eggs into male's pouch; 3. After gestation period, male shoots or pumps babies out of his pouch. (Illustration by Gillian Harris)

genera), Centriscidae (three genera), Aulostomidae (four genera), and Fistulariidae (some three genera and four spp.). The actual number of species from Monte Bolca is difficult to estimate with precision, but this formation represents the greatest extinct diversity of the order. The gasterosteiform species present in both the Nardò and Monte Bolca deposits were inhabitants of the former Tethys Ocean, which separated the extinct continents Laurasia and Gondwana during much of the Cretaceous and Tertiary periods. Other fossils, mostly represented by fragmentary material and allied to the Aulostomidae and Fistulariidae, are known from Turkmenia, in deposits almost contemporaneous with Monte Bolca. Fossil sticklebacks have been found in the Tertiary of California (Monterey Formation) and Siberia. Tertiary pipefishes have been described from the Modelo and Puente Formations of southern California as well as from the Caucasus and Carpathian Mountains of eastern Europe.

Physical characteristics

The morphological characteristics of various gasterosteiform families are highly modified and specialized; some of the members of this order are among the most morphologically interesting of all fishes. Some forms are more pelagic and streamlined (e.g., aulorhynchids), whereas others

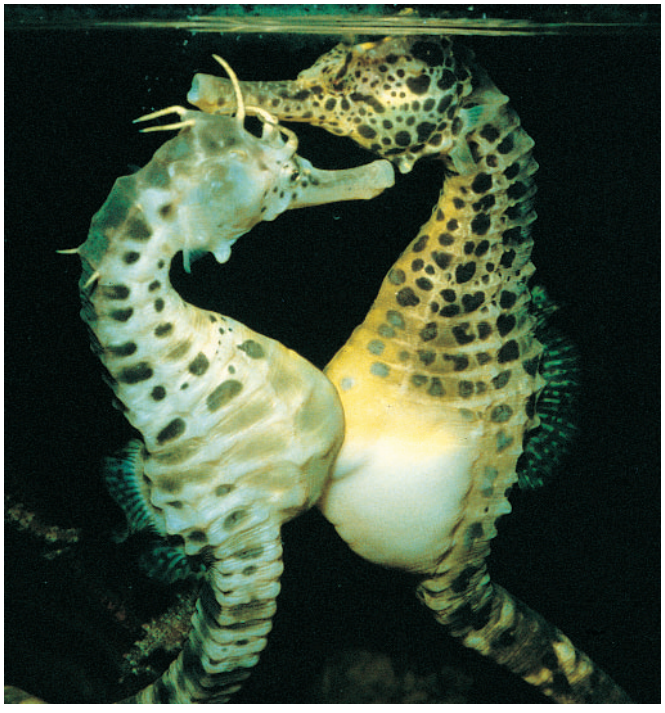
A threespine stickleback (*Gasterosteus aculeatus*) male deposits his sperm in the nest after a female has spawned. (Photo by Animals Animals © D. Thompson, OSF. Reproduced by permission.)

are benthic and highly cryptic (e.g., pegasids). Many forms are elaborately camouflaged and blend in perfectly with their surroundings (some of the most notable examples are *Syngnathus typhle*, *Solenostomus cyanopterus*, and *Histiogamphelus cristatus*); some syngnathid species have been discovered only after their particular substrate was collected and examined. Additionally, some species carry algal growths and complex dermal projections that further aid in their concealment (the most striking example may be the leafy seadragon *Phycodurus eques*), and many species have the ability to change color at will (e.g., *Aulostomus chinensis*). Most species have the head and body on the same plane, as in "typical" fishes, but seahorses have the head at more or less a right angle to the body, a unique condition among fishes.

There is much morphological variation among the families and subfamilies, and many are recognized easily by their unique designs. Gasterosteids (sticklebacks) resemble more "typical fishes," with an unmodified head and clearly demarcated fins, but most gasterosteiforms have elongated snouts, with small upturned mouths, and may lack some fins or even all of them (*Bulbonaricus*). The snout may be absent (*Bulbonaricus*); truncated (*Histiogamphelus*); mildly elongated (*Indostomus*); or very long and tubular, reaching up to one-third of their total length (e.g., *Aulostomus* and *Fistularia*). The mouth usually is very small, located at the end of the snout (except in pegasids, where the mouth is underneath the snout), and most species lack teeth. The eyes typically are round and vary from large to small. Most species have very slender and elongated bodies, but gasterosteoids (except *Indostomus*) and some syngnathoids (e.g., Macroramphosidae, Centriscidae) are laterally compressed.

The fins typically are highly modified. They have either one or two dorsal fins; the single dorsal fin may be preceded by numerous spines (gasterosteoids, *Aulostomus*), but in some forms the spines represent the first dorsal fin (*Solenostomus*, centriscids, and macroramphosids). In most species, however, there is a single dorsal fin with soft rays only. Pelvic fins are absent in *Hypoptychus* and syngnathids, and the caudal fin is absent in most syngnathids. Many syngnathids have prehensile tails that enable them to cling to soft corals and algae. Most gasterosteiforms are covered in bony plates, scutes, or rings and have numerous elaborate dermal projections on the head, body, and tail. There is also great morphological variation internally (e.g., lack of true stomachs in seahorses and reduction of the number of cephalic bones in many species). Details of the morphological features of the different families are elaborated in the species accounts.

Gasterosteiforms are among the most colorful fishes, displaying a wide spectrum of colors and patterns. There is also much diversity in coloration within certain species, and some individuals may change color while breeding or to blend into different backgrounds. Every conceivable color pattern seems to be present within the order, as some species combine strong colors (e.g., red, orange, yellow, green, white, black, and blue) with spots, blotches, ocelli, mottlings, and stripes of various kinds. Gasterosteiformes also vary considerably in size, from some 0.8 in (2 cm) in length among pygmy seahorses to more than 4.9 ft (1.5 m) for cornetfishes (*Fistularia*).



A big-bellied seahorse (*Hippocampus abdominalis*) female deposits eggs into a male's pouch. (Photo by Animals Animals ©R. Kuiter, OSF. Reproduced by permission.)

A leafy seadragon (*Phycodurus eques*) near Kangaroo Island, Australia. Unlike seahorses, seadragons do not have a pouch for rearing the young. Instead, the male carries the eggs fixed to the underside of his tail until they hatch. (Photo by Animals Animals ©James Watt. Reproduced by permission.)

Distribution

Worldwide in tropical and temperate marine waters as well as in temperate freshwaters of the Northern Hemisphere. Species are more abundant in the tropical Indo-West Pacific region, where several undescribed pipefish species are known. Some species are widespread (e.g., the red cornetfish, *Fistularia petimba*), whereas others are very restricted in distribution (e.g., *Festucalex cinctus* off central New South Wales and southern Queensland, Australia). A few species with wide distributions, such as *Hippocampus erectus* and *Doryrhamphus dactyliophorus*, may require subdivision.

Habitat

Most species are coastal residents, present in shallow continental shelf areas in a variety of habitats, such as coral reefs, atolls, offshore reefs, sea grass meadows, kelp forests, tide pools, estuaries, bays, and lagoons and over sandy or muddy bottoms. Many species live cryptically, hiding among rocks and crevices in reefs or blending in with gorgonian corals or sea grasses. Many species have pelagic young, which eventually settle closer to the bottom. Some 20 gasterosteiform species are freshwater (at least one stickleback is exclusively so, along with *Indostomus* and pipefishes of the genera *Microphis*, *Hippichthys*, and *Dorichthys*) and are present in a variety of habitats, including lakes, coastal rivers, creeks, marshes, and protected coastal inlets. Some 40 species are euryhaline, found in brackish environments. As far as is known, no species occurs in deep-water environments.

Behavior

Gasterosteiforms are diurnal as far as is known. Most species are solitary or live in pairs or small groups or sometimes in larger groups (e.g., aulorhynchids). Many species have pelagic young, but most adults are benthic. A few species, such as macroramphosids and aulorhynchids, form schools, sometimes containing thousands of individuals. Most species remain in association with soft corals, hard corals (*Hippocampus barbouri*), algae, sea grasses, or other substrates, where they

A short-nosed seahorse (*Hippocampus breviceps*) male giving birth. (Photo by Animals Animals ©R. Kuiter, OSF. Reproduced by permission.)

are well camouflaged; in many cases they grasp the reef with their prehensile tails. Many species appear sluggish owing to their somewhat sedentary lifestyle and lack of ability to move very swiftly. Syngnathids swim by a combination of movements of their pectoral and dorsal fins, and some species swim by moving their tails from side to side. Many syngnathids appear to hover in one location, controlling their position by coordinated movements of their pectoral and dorsal fins. Some pipefishes (e.g., *Heraldia*) are able to swim in an upside-down position in caves and crevices. Centriscids remain in a vertical position, with their mouths directed toward the bottom, sometimes in association with urchins. Species of pipefishes, *Solenostomus*, *Aulostomus*, and macroramphosids also maintain a vertical position at times. Many species can change their coloration according to their background, using this ability to sneak up on prey or to hide from predators. Some species, especially pipefishes (e.g., *Doryrhamphus* spp.), have been documented to clean other fishes (e.g., moray eels and damselfishes), removing their parasites while in reefs.

Feeding ecology and diet

Most syngnathoids feed on a wide variety of small crustaceans (e.g., copepods and mysids), sometimes almost exclusively, as well as on other small invertebrates and the larvae of other fishes. The larger species, such as cornetfishes and trumpetfishes, also feed on larger fishes. Most gasterosteiform species ingest prey whole by quickly opening their mouths to produce a strong inward current, a suction mechanism called pipette feeding. In this manner, large prey items cannot be ingested, owing to the small terminal mouths, lack of teeth, and tubular snouts of many syngnathoid species. Most prey items are ingested from the substrate or when just hovering above it. Many gasterosteiforms rely on their highly developed camouflage to surprise prey items. This is the case in numerous species of pipefishes that slowly cruise over sandy bottoms with sea grasses, feeding on small crustaceans that fail to perceive them as a result of their cryptic appearance. Many species feed on small mysids and other crustaceans that are more free-swimming as well as fish larvae; they remain in strategic positions along the fringes of reefs, where they are exposed to currents that may contain these prey items. Some species, however, eat primarily in the water column (e.g., macroramphosids and aulorhynchids). Gasterosteiforms are preyed upon by larger carnivorous fishes, such as flatheads (Platycephalidae) and snappers (Lutjanidae). Because they move slowly, gasterosteiforms are ingested easily once they are discovered.

Reproductive biology

A great variety of reproductive strategies occur in this order, including some of the most elaborate known for any group of fishes. In a few families (Centriscidae, Macroramphosidae, Pegasidae, and perhaps Aulorhynchidae), the eggs and larvae are pelagic, and spawning probably is accomplished (at least in some of these families) in a style similar to broadcast spawning, in which eggs and sperm are released directly into the water column. In pegasids, spawning involves a courtship ritual whereby a female and a male swim vent to vent, releasing eggs and sperm simultaneously. In other families, reproduction is a far more complex process in which the male carries the eggs, sometimes in a special pouch, within which the eggs may be fertilized. In *Solenostomus*, the females carry the fertilized eggs in pouches made of their greatly extended pelvic fins, repeatedly opening and closing them to fan the eggs. As a preliminary behavior to spawning, many species employ complex courtship rituals, in which males compete for the female by dancing, inflating their pouches, or performing in some other way. A male stickleback lures the female into his nest and fertilizes the eggs there, sometimes attracting several females in succession. Some species are reproductively active throughout the year, whereas others are seasonal. Many species of syngnathids form monogamous pairs.

A ringed pipefish (*Doryrhamphus dactyliophorus*) over lava sand in the Lembeh Strait, Sulawesi, Indonesia. (Photo by Fred McConnaughey/ Photo Researchers, Inc. Reproduced by permission.)

Reproduction has been studied in detail for many syngnathids. In seahorses, the females insert their eggs into the pouch of the males, using an abdominal projection known as the ovipositor (an everted egg duct); the eggs are fertilized by the sperm located in the pouches. During this process the male and female face each other. Inside the pouch the eggs are enveloped in tissue that supplies oxygen to the eggs (through diffusion from capillaries) as well as hormones by bathing the small portion of the egg that protrudes from the surrounding tissue. The pouch remains sealed. The male carries the eggs to term (incubation may last from 10 days to six weeks, depending on the species and surrounding temperature), during which time he appears very pregnant. The male

actively expels the young (by forcefully moving back and forth) over a period of a few hours through an opening at the top of the pouch. Usually, about 100 young are born in this manner, but some species produce up to 400 young, whereas others produce between 10 and 50 (measuring close to 0.4 in, or 1 cm); pairs may have several broods in one year. The young do not receive any further parental care and are on their own immediately after birth. Young may congregate, and their sexes can be distinguished after a few months, when the pouches of the males become apparent (i.e., when they become sexually mature). Young resemble adults shortly after birth. As many as 1,000 young are produced per year by each couple in this manner, although the actual number varies between species, as reproduction may occur continuously.

Many pipefish males carry the eggs in the anterior tail region (just underneath the dorsal fin) without enclosing them in a pouch, fertilizing the eggs when they are deposited. The eggs are clearly visible in these cases. Courtship has been observed in detail in the species *Corythoichthys isigakius* from Japan. In this species, after a couple has consented to mate, the male and female repeatedly circle each other with their heads raised, exposing their undersides while remaining in an almost vertical position. When the male is ready to incubate the brood and the female is full of eggs, they practice egg transfer for several days until the process is actually enacted. The male's tail is flattened laterally as an indication that he is able to receive the eggs. The female places her small, greenish eggs on his tail, pushing them into place so that they remain attached. The eggs hatch after a few weeks. Hatching may be helped by the male, who shakes vigorously until all the eggs have separated. The young then are ready to begin their short pelagic life.

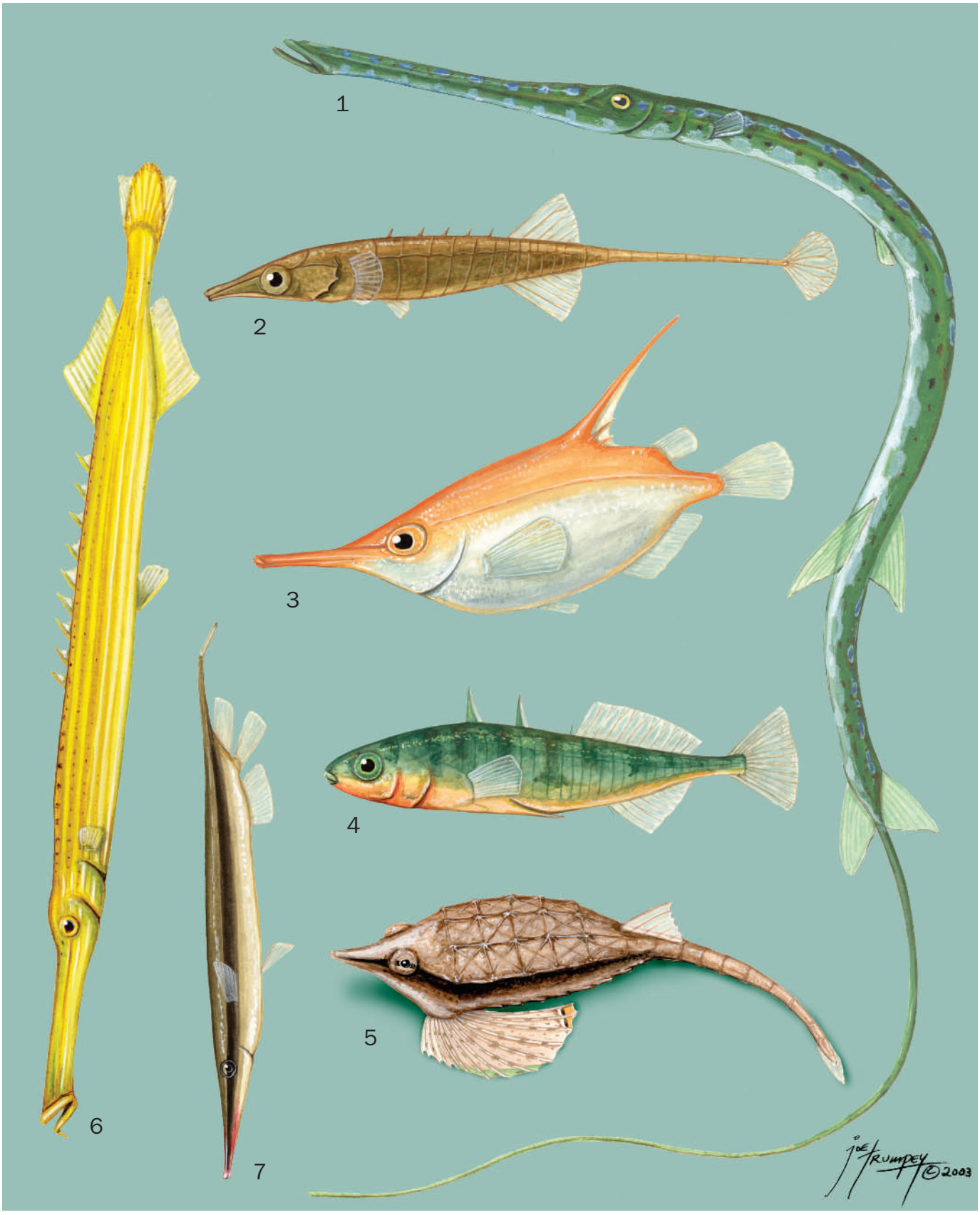
Conservation status

A relatively large number of gasterosteiform species are listed by the IUCN. Most of the threats that these species face are related to the pervasive seahorse trade, especially in southeastern and eastern Asia, and to widespread habitat degradation. Gasterosteiforms generally are not directly consumed in quantities that would otherwise place them in danger of overexploitation. Overexploitation of seahorses is a result of their use as ingredients for prepackaged medicines, where demand far exceeds supply, and for the curio and aquarium trade. Many species live in coastal or estuarine habitats, which typically are more affected by development and pollution. Furthermore, the vulnerability of seahorses is enhanced by their low fecundity, parental care, and complex social structures. The IUCN presently includes in their compilation of threatened taxa about 51 species of gasterosteiformes. The majority of species are listed either as Data Deficient or Vulnerable (all species of seahorses and many species of pipefishes). The Cape seahorse (*Hippocampus capensis*) is listed as Endangered (mostly due to commercial development of its restricted habitat), and the stickleback (*Pungitius hellenicus*) and the river pipefish (*Syngnathus watermeyeri*) are listed as Critically Endangered. Conservation efforts, mostly geared toward seahorses, are presently being undertaken by Project Seahorse, a praiseworthy initiative that aims to promote the sustainable exploitation of seahorses and their relatives.

Significance to humans

Numerous species of this order are popular fishes sought out by recreational divers. Many are important aquarium fishes and, fortunately, are now reared in captivity. Their popularity stems from their complex and highly modified morphological features and ornate coloration as well as the particular breeding habits of various species, in which there are elaborate courtship rituals and males fertilize the eggs and carry the young (in most species). Gasterosteiforms typically are not consumed as food fishes, but some syngnathids are commercialized heavily as curios. In particular, seahorses and seamoths are made into souvenirs (even as Christmas ornaments) and used as ingredients in traditional Chinese and related East Asian medicines. Some 47 countries worldwide participate in the seahorse market, and the total global consumption of seahorses in 1995 was at least 20 million specimens, roughly more than 62 tons (56 metric tonnes). The seahorse trade is not sustainable as it is currently implemented, leading to fears that many populations of seahorses have been exploited past the possibility of recovery.

1. Ringed pipefish (*Doryrhamphus dactyliophorus*); 2. Leafy seadragon (*Phycodurus eques*); 3. Weedy seadragon (*Phyllopteryx teaniolatus*); 4. Female lined seahorse (*Hippocampus erectus*); 5. Ornate ghost pipefish (*Solenostomus paradoxus*). (Illustration by Joseph E. Trumpey)



1. Blue-spotted cornetfish (*Fistularia tabacaria*); 2. Armored stickleback (*Indostomus paradoxus*); 3. Longspine snipefish (*Macroramphosus scolopax*); 4. Threespine stickleback (*Gasterosteus aculeatus*); 5. Sculptured seamoth (*Pegasus lancifer*); 6. West Atlantic trumpetfish (*Aulostomus maculatus*); 7. Common shrimpfish (*Aeoliscus strigatus*). (Illustration by Joseph E. Trumpey)

Species accounts

West Atlantic trumpetfish
Aulostomus maculatus

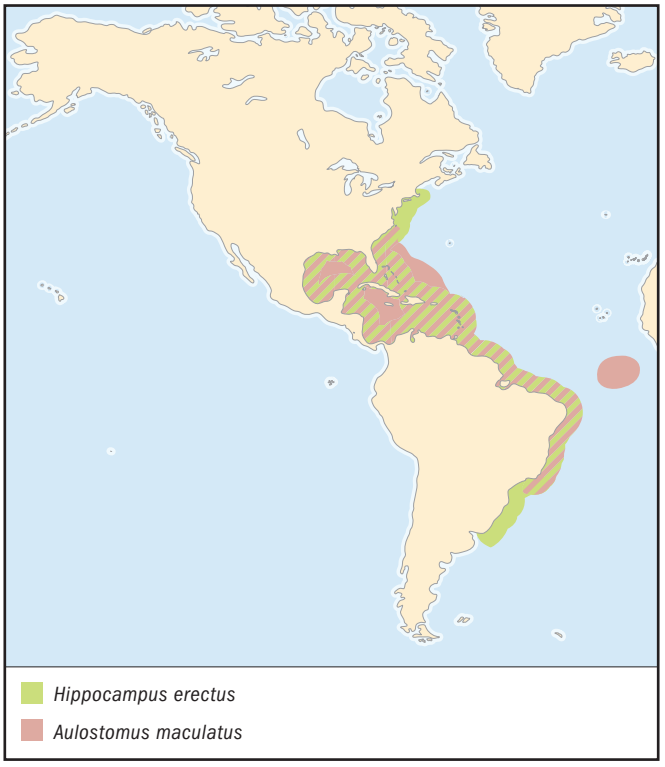
FAMILY
Aulostomidae

TAXONOMY
Aulostoma maculatum Valenciennes, 1837, West Atlantic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The trumpetfish is slender and elongate. The head is about one-third of the total length; the snout is tubular and the mouth large, terminal, and very upturned. The chin has a prominent barbel, and the eyes are relatively small and round. Single dorsal fin is preceded by eight to 13 short, well-spaced spines. Dorsal fin with 21–25 rays; anal fin opposite to dorsal fin and also with 21–25 rays; pelvic fins very posterior. Scales small and somewhat abrasive. Reaches at least 35.4 in (90 cm) in length. Coloration varies. May have dusky brown or reddish background with lighter stripes and darker spots, but some individuals are yellow or green with a blue snout.

DISTRIBUTION
Western Atlantic from Florida to southeastern Brazil; also in the Caribbean, Gulf of Mexico, Bermuda, and Antilles. Found in the eastern Atlantic at Saint Paul's Rocks.



HABITAT
Adults usually are found in coral reefs and associated habitats, at depths ranging from 6.6 to 82 ft (2–25 m); juveniles live in deeper water but also among sargassum.

BEHAVIOR
Trumpetfishes may hover in near vertical positions, with their heads pointing downward, sometimes almost motionless. They align their bodies with other linear objects, ranging from corals to other fishes to crevices, blending in with their surroundings. They also are capable of quick movements. Reported to change color according to their habitat. They also use larger non-piscivorous fishes such as parrotfish as mobile blinds, hiding behind them to approach within striking distance of prey.

FEEDING ECOLOGY AND DIET
Eats mostly smaller fishes and small invertebrates by employing stealthy movements and suction feeding (pipette feeding). May feed on larger fishes as well.

REPRODUCTIVE BIOLOGY
Mostly unknown; juveniles are known to inhabit deeper waters, but eggs and larvae probably are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes kept in public aquaria. A harmless fish, sometimes marketed locally but of minor commercial importance. ◆

Common shrimpfish
Aeoliscus strigatus

FAMILY
Centriscidae

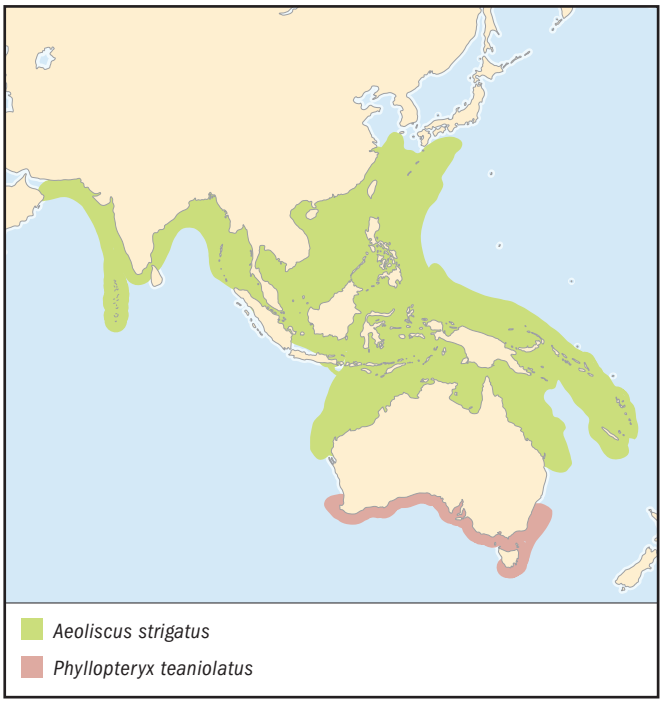
TAXONOMY
Amphisile strigata Günther, 1861, Java, Indonesia.

OTHER COMMON NAMES
English: Razorfish.

PHYSICAL CHARACTERISTICS
A very unusual species, with an elongate, highly compressed body. Snout long, almost filamentous, with a terminal mouth. Dorsal fin terminal, situated far posterior, with a long, posteriorly directed and hinged spine followed by two smaller spines and nine to 10 rays. Caudal fin underneath dorsal fin. Anal fin with 11–12 rays; pectoral fin with 11–12 rays. Body covered in plates. Coloration yellowish dorsally and laterally above a dark, horizontal stripe that runs through the eyes; white underneath stripe and ventrally. Reaches 5.5 in (14 cm) in length.

DISTRIBUTION
Widespread in the tropical western Pacific Ocean and northern Indian Ocean, reaching as far west as the Seychelles.

HABITAT
Usually found in shallow bays, coral reefs, and sea grass beds down to a depth of about 66 ft (20 m).



BEHAVIOR
Commonly encountered in large schools, typically hovering with its mouth pointed toward the bottom, maintaining a vertical position. Sometimes found in association with long-spined sea urchins of the genus *Diadema*.

FEEDING ECOLOGY AND DIET
Feeds on small invertebrates (e.g., polychaetes), including larvae of mollusks and crustaceans.

REPRODUCTIVE BIOLOGY
Mostly unknown. Pelagic larvae have been described and begin to resemble adults by about 0.7 in (17 mm) in length.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not consumed but sometimes kept in aquaria. ◆

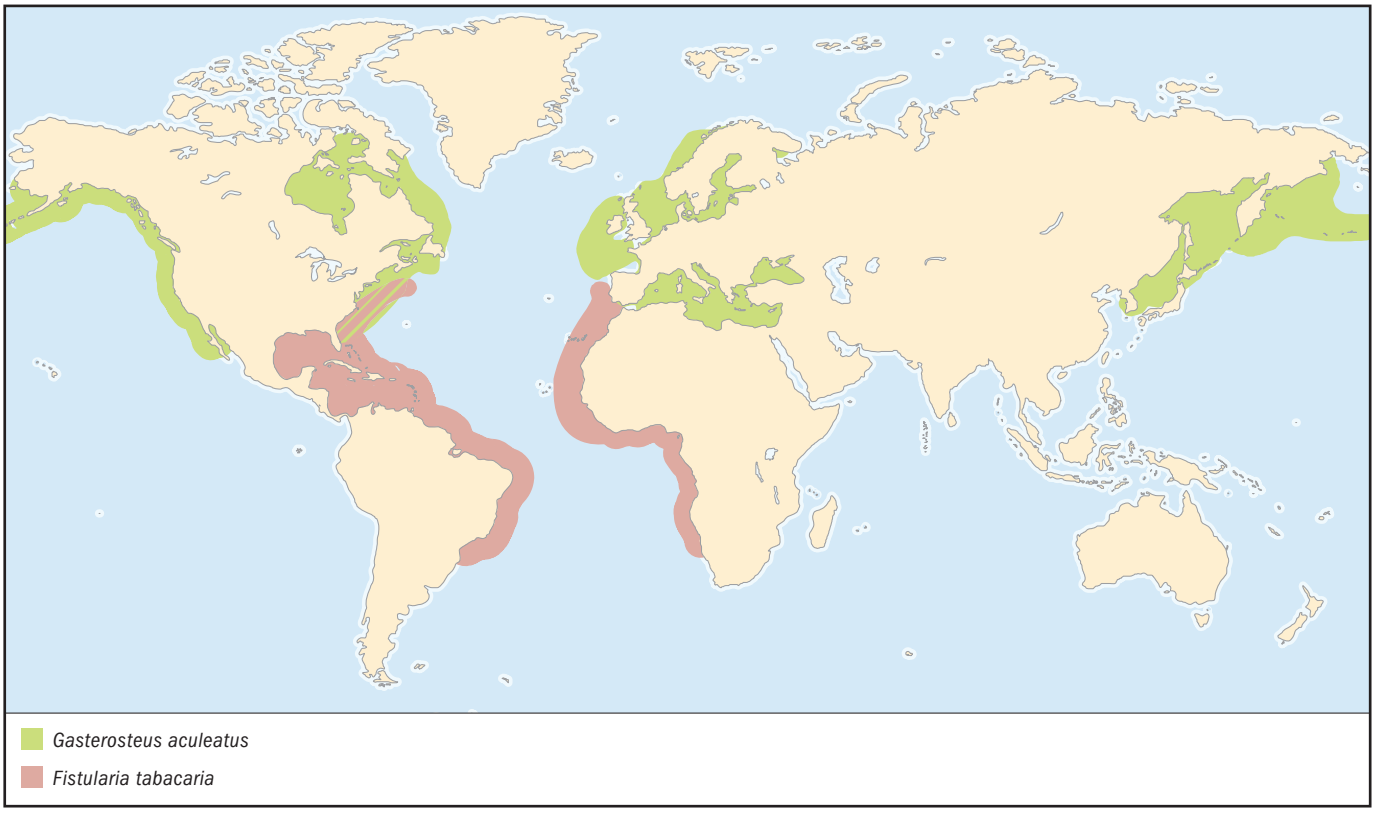
Blue-spotted cornetfish
Fistularia tabacaria

FAMILY
Fistulariidae

TAXONOMY
Fistularia tabacaria Linnaeus, 1758, North Atlantic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
An unmistakable species, with an extremely elongated body and snout (about one-fourth of the body length). Oblique terminal mouth with many minute teeth. Eyes elliptical and large. Small, single, and triangular dorsal fin located far posterior on the back, opposite to the anal fin and with 13–18 rays. Anal fin also triangular, with 13–17 rays. Pectoral fins have 15 or 16



rays. Very small pelvic fins. Caudal fin has two clear forks, with upper and lower lobes divided by a long caudal filament (formed from caudal rays, about as long as the snout). Coloration is greenish brown, with numerous blue spots and some 10 darker cross bars. Caudal filament is blue (coloration can change quickly to mach the background). Reaches up to 5.9 ft (1.8 m) without the caudal filament.

DISTRIBUTION
Occurs in both sides of the tropical and warm temperate Atlantic Ocean. Young are reported to venture into colder temperate waters as far north as Nova Scotia in the Western Atlantic.

HABITAT
A mostly inshore species, occurring down to 656 ft (200 m); adults are found in coral reefs and sea grass meadows, over sandy and rocky bottoms, and even in estuaries.

BEHAVIOR
Mostly unknown. This species does not seek camouflage by aligning itself with objects, as does the trumpetfish. Usually solitary.

FEEDING ECOLOGY AND DIET
Eats mostly small shrimps and other fishes, which it can swallow whole, head first (by sucking them in a mode known as pipette feeding). Preyed upon by larger bony fishes (e.g., groupers) and sharks.

REPRODUCTIVE BIOLOGY
Little is known of its reproductive biology, but other species of *Fistularia* lay pelagic eggs in open waters; larval development probably is pelagic as well.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not frequently consumed but a popular aquarium species. ◆

Threespine stickleback
Gasterosteus aculeatus

FAMILY
Gasterosteidae

TAXONOMY
Gasterosteus aculeatus Linnaeus, 1758, Europe.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Head relatively small, with small upturned mouth anterior to the eyes; eyes round and somewhat large. Body about four times as long as it is deep, with slender caudal peduncle. Three strong spines precede the first dorsal fin (with 10–14 rays), the last of which is smaller and attached to the dorsal fin; the first two spines are very tall. Dorsal spines are widely spaced. Anal fin opposite soft dorsal fin, with one spine and eight to 10 rays. Pectoral fins ending at mid-body length, with 10 rays. Pelvics have strong spine and single ray. All spines can be locked into place or depressed. Caudal fin brush-shaped. Trunk covered by slender plates, with much variation in arrangement. Coloration silvery on sides and bluish black dorsally, with orange pelvic membranes. Males become more reddish when courtship commences and drab when it terminates. Reaches 3.5 in (90 mm) in length.

DISTRIBUTION
Widely distributed in temperate marine waters of the Northern Hemisphere but also in coastal rivers and lakes.

HABITAT
The threespine stickleback occurs in a wide variety of coastal habitats in both brackish and shallow marine waters. It can be captured occasionally in the open ocean as well. Typical habitats include tidal pools, coastal rivers and creeks, lakes, salt marshes, and protected coastal inlets. Adults typically are found in association with vegetation (e.g., eelgrass). Individuals may venture far out into the open oceans, as far as 621 mi (1,000 km) in the Pacific.

BEHAVIOR
Many populations remain most of the time in the open sea, venturing into coastal habitats to spawn and die in their second or third years. They swim by "rowing" with their pectoral fins and are capable of strong swimming motions, such as those required to ascend rivers. Moderately social outside of periods of reproductive activity, when males become strongly territorial.

FEEDING ECOLOGY AND DIET
Eats a wide variety of invertebrates and larvae, including copepods, gammarids, rotifers, branchiurans, oligochaetes, insects and their larvae, and even eggs of other sticklebacks. Sticklebacks are preyed upon by numerous other fishes as well as water birds, such as herons, mergansers, gulls, and loons.

REPRODUCTIVE BIOLOGY
The reproductive biology of this species has been studied in detail. Females from 2 to 2.8 in (5–7 cm) in standard length have between 116 and 838 eggs, measuring about 0.06 in (1.5 mm) in diameter; egg number increases with body weight. Before spawning, males establish a territory, building a nest on the substrate (which is accomplished by "gluing" together bits of vegetation with mucus and kidney secretions). The nest is complete when the male carves out a tunnel, at which time courtship begins. A dance is performed for a gravid female that has entered the territory, which consists of the male jumping toward and away from the female in a zigzag fashion, with spines erect and mouth open. Once a female is impressed, the male exhibits gluing behavior and fans the nest with his pectoral fins. He then zigzags back to the female, leads her to the nest, and points to it with his open mouth. The female enters the nest with her caudal peduncle protruding, allowing the male to begin quivering movements against her flank. After she has deposited her eggs, the male moves through the nest, fertilizing the eggs and expelling the female. He then pushes the eggs deeper into the nest, flattening the egg mass and repairing the nest at the same time, before fanning the eggs. The male attempts to induce other females to spawn in the same nest; the number of female partners may vary, but studies conducted in Quebec indicated that males having two or three female partners is the norm in that region. Incubation lasts roughly 14–20 days. After the eggs hatch, the male destroys the nest and guards the young (collecting any that may have fallen away). After his progeny become free-swimming, the male starts another courtship cycle.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not a commercially important species. The threespine stickleback is studied intensely by fish ethologists. Often kept in aquaria, where it reproduces easily. ◆

Armored stickleback

Indostomus paradoxus

FAMILY
Indostomidae

TAXONOMY
Indostomus paradoxus Prashad and Mukerji, 1929, Lake Indawgyi, Myanmar.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body elongate and slender, with a spatulate snout and terminal mouth. Eyes large and round. The single dorsal fin contains six rays, is located at mid-body length, and is preceded by five short and evenly spaced spines. The anal fin is opposite the dorsal fin, also with six rays. The caudal fin contains 11 rays and is rounded posteriorly. Pelvic fins are very small and thoracic, with only four rays. The precaudal tail region is very long and slender. Large pectoral fins have 23 rays. Body is covered by a complex armor composed of numerous plates. Coloration is a light brown, with numerous small, darker blotches and irregular stripes. Reaches 1.2 in (3 cm) in length.

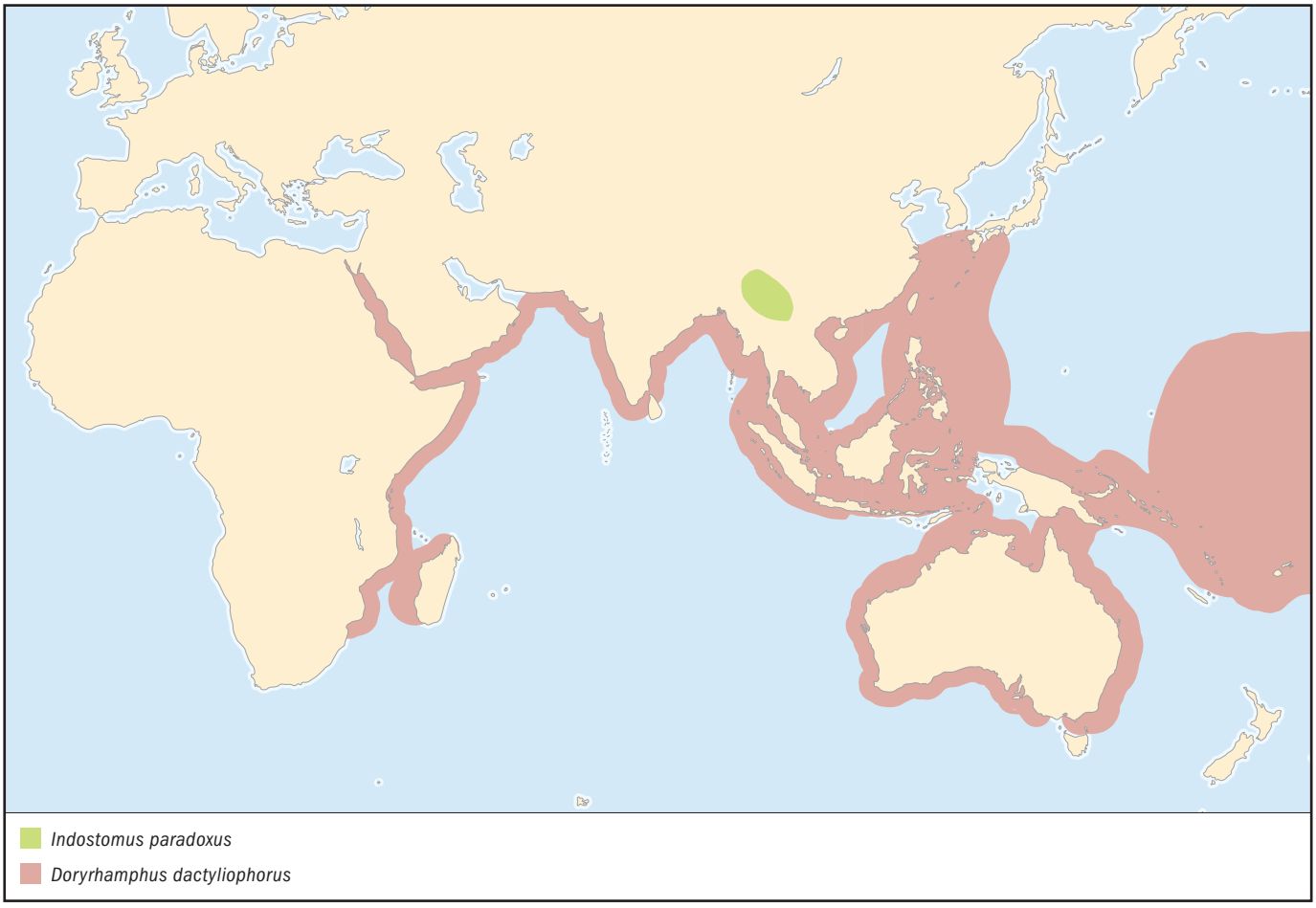
DISTRIBUTION
Northern Myanmar, possibly to Cambodia.

HABITAT
Rivers and lakes of northern Myanmar, including the Ayeyarwaddy River and Lake Indawgyi. Occurs close to the bottom in canals, swamps, ditches, and stagnant waters.

BEHAVIOR
Mostly unknown. This species apparently is sedentary in river or lake beds and moves about slowly.

FEEDING ECOLOGY AND DIET
Feeds mostly on worms and other small, slow-moving benthic invertebrates. Predators are presumably larger fishes.

REPRODUCTIVE BIOLOGY
The reproduction of this species has been observed under captive conditions. Males defended spawning sites of a few centimeters inside a tube and had a lighter reddish brown coloration (instead of the typical darker brown color of nonbreeding males). There is sexual dimorphism in the pelvic fins: males have longer and wider pelvics with inward curving rays. Males displayed by erecting their fins and shaking their tail regions. Females are lighter brown during spawning, with bulging abdomens due to the presence of eggs. Females approached the nesting sites of the male when they were about to spawn (indicated by their protruding genital papillae) and were encouraged to enter the tube by the male. The upside-down female deposited eggs, usually on the roof of the tube; the male fertilized the eggs while also upside-down. Spawning may take several hours, and the male guards the nest. From five to



40 elliptical eggs were laid at a time, measuring about 0.08 in by 0.04 in (2 by 1 mm). Eggs hatched three days after spawning, and larvae were free-living four days after hatching, at about 0.14 in (3.5 mm). Larvae have an attachment organ on the tip of the yolk sac. Larval coloration is unique, composed of three black vertical bands, and adult coloration is attained after more than four weeks and at about 0.3 in (8 mm) in length.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally imported as an aquarium species. ◆

Longspine snipefish
Macroramphosus scolopax

FAMILY
Macroramphosidae

TAXONOMY
Balistes scolopax Linnaeus, 1758, Mediterranean Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body is compressed laterally, with an elongated, tubular snout that terminates in a small upturned mouth lacking teeth. Eyes are round and large, with a single nostril on each side. Two dorsal fins, originating far posteriorly. First dorsal has extremely elongated and serrated second spine (four to eight spines, with each spine about as long as the snout); second dorsal fin has soft rays (10–14). Anal fin has 19–21 rays, pectoral fin has 18–21 rays, and pelvic fins have a single spine and four rays. Scales are very small. Pinkish or reddish dorsally; color fades to silvery on the sides. Reaches 9.1 in (23 cm) in total length.

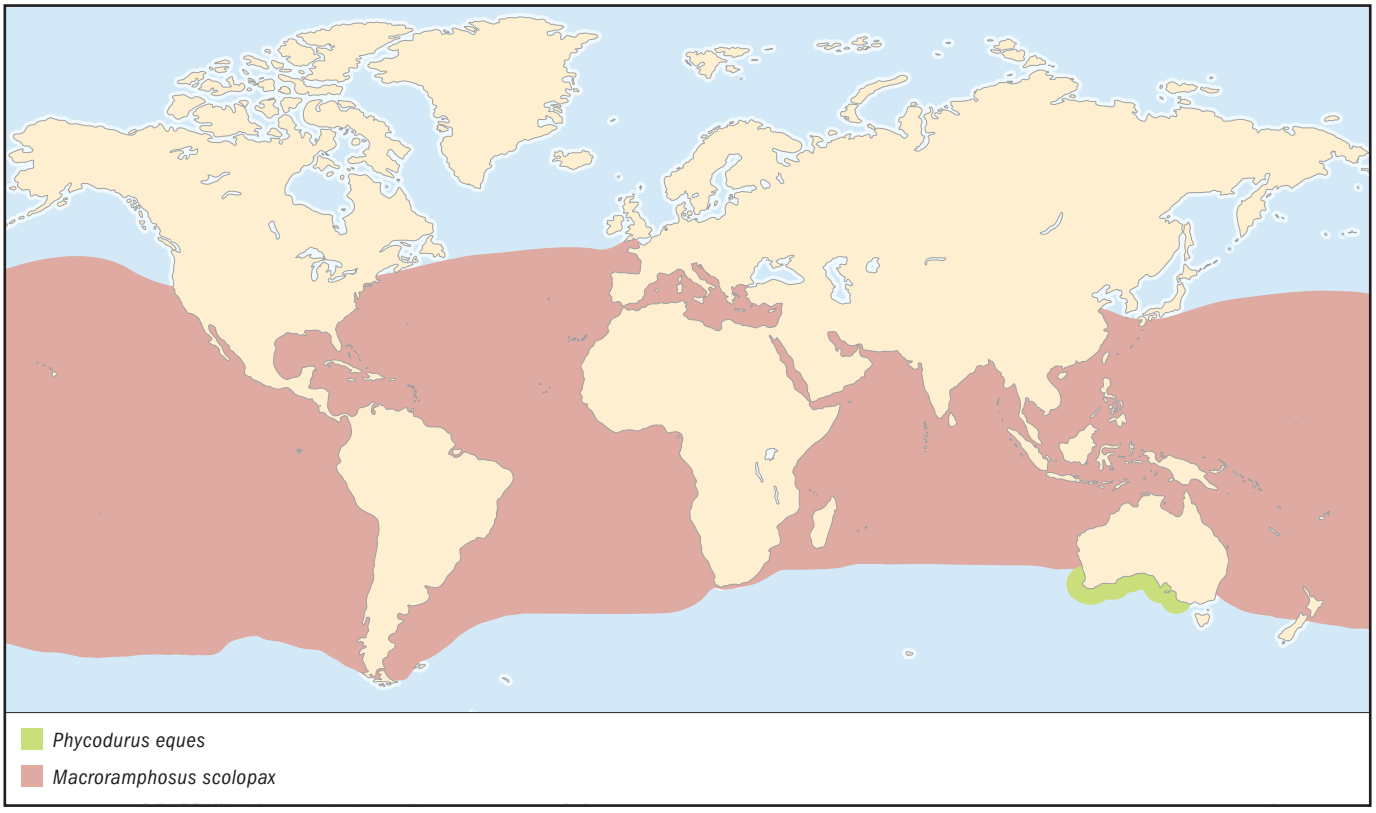
DISTRIBUTION
Distributed worldwide, mostly in temperate latitudes.

HABITAT
Present mostly on the continental shelf in depths ranging from 164–902 ft (50–275 m). Juveniles are more pelagic, whereas adults are more demersal.

BEHAVIOR
Forms large schools, mostly while juvenile. Individuals may hover with their mouths pointing down toward the substrate, remaining in a stationary position.

FEEDING ECOLOGY AND DIET
Feeds on invertebrates, including copepods and other crustaceans, mollusk larvae, foraminifera, polychaete eggs, and mysids. Preyed upon by larger fishes, including tunas and blue sharks.

REPRODUCTIVE BIOLOGY
Eggs and larvae are pelagic, as are juveniles until they reach about 2 in (5 cm) in length. Adults are more demersal. In the eastern Atlantic, snipefish spawn on the continental shelf, over seamounts, and near islands between October and March. Larvae and juveniles remain in the surface layers during the day but migrate vertically to deeper water at night. At about 2 in (5 cm), some three months old, individuals move closer to the bottom.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not very important commercially, although it is consumed in the eastern Atlantic. This species has been kept in public aquaria. ◆

Sculptured seamoth
Pegasus lancifer

FAMILY
Pegasidae

TAXONOMY
Pegasus lancifer Kaup, 1861, Australia.

OTHER COMMON NAMES
None known.

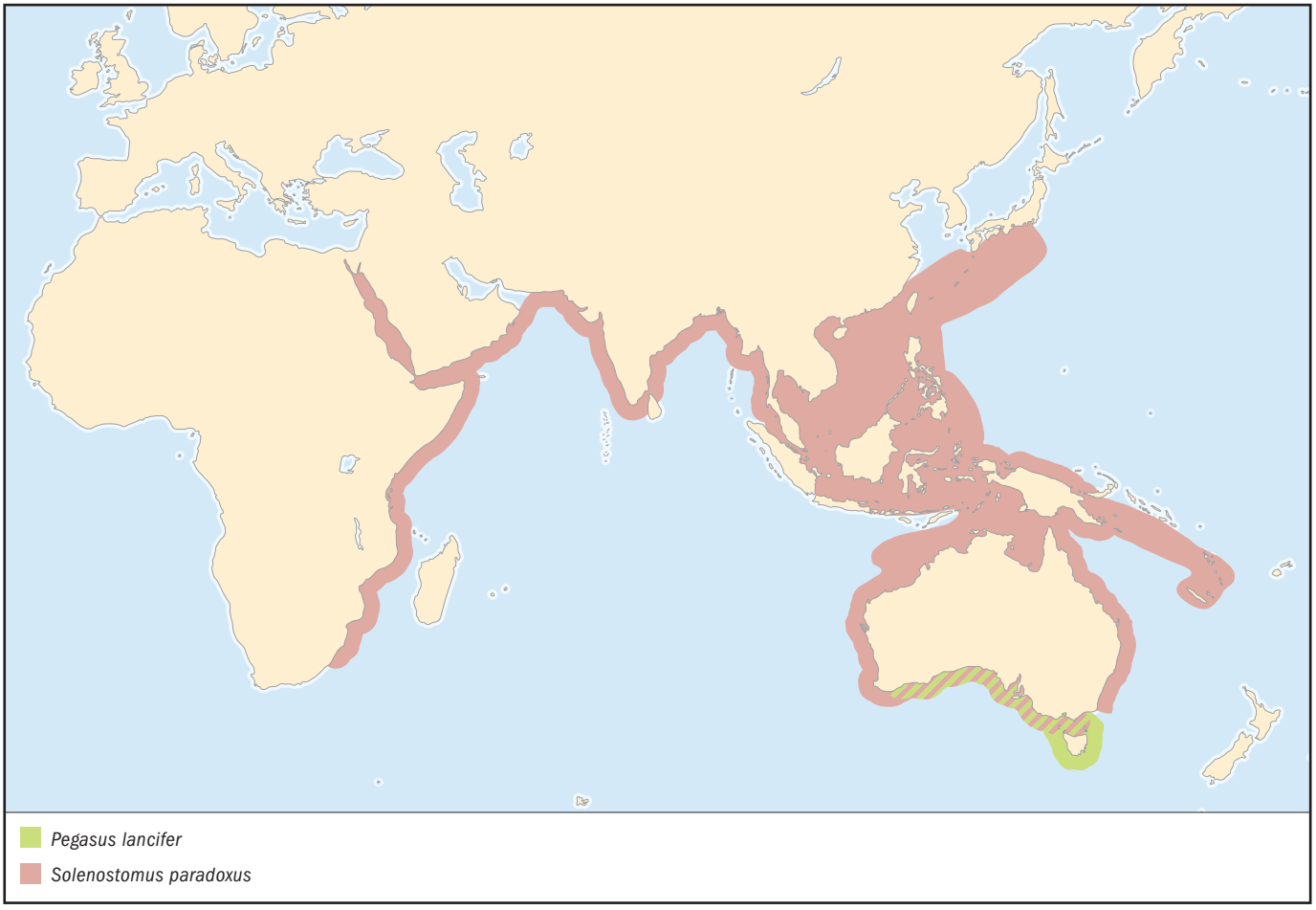
PHYSICAL CHARACTERISTICS
Snout very slender but not very elongated (longer in males), ending in a spatulate tip; snout clearly demarcated from head and bearing four spiny ridges. Eyes large and round. Mouth small and protrusible, located ventral to the snout base. Head triangular anteriorly. Head and trunk regions are depressed and broad (broader in females), encased in fused bony plates that bear prominent ridges forming a star pattern. Single dorsal fin posterior to the trunk, with five rays; opposite anal fin also has five rays. Tail long and slender, with bony ridges, ending in a truncate caudal fin with eight to nine rays. Pectoral fins very wide and fanlike when expanded, with 18 rays. Pelvics resemble hooks, with one spine and three rays. Coloration sandy-brown or grayish above, with darker spots on pectorals, a dark longitudinal stripe on the trunk, and a dark stripe at base of the tail; pale underneath. Reaches about 4.7 in (12 cm) in length.

DISTRIBUTION
Restricted to southern Australian waters from South Australia to Tasmania.

HABITAT
A bottom-dwelling species occurring in many different coastal habitats, including estuaries, sea grass beds, and sandy bottoms, down to about 180 ft (55 m).

BEHAVIOR
This species can change its color to match that of its surroundings. It also can burrow into the substrate to escape predators. It often "walks" or "crawls" over the bottom in search of small crustaceans or other food items. Many individuals may congregate in estuaries.

FEEDING ECOLOGY AND DIET
Eats a variety of small invertebrates, such as polychaetes, mollusks, and crustaceans. Their mouths are somewhat protrusible,



enabling them to snatch prey from the bottom with ease. Presumably eaten by larger fishes.

REPRODUCTIVE BIOLOGY
Enters sandy bays to breed in the spring, when courtship takes place. During courtship, a female and male remain on the bottom, side by side, until they rise together to spawn, vent to vent, about 3.3 ft (1 m) off the bottom. The posterior tips of the pectoral fins of males become yellow during the reproductive period. The eggs are pelagic, and larvae up to 0.1 in (2.5 mm) are enclosed in a dermal sac, probably an adaptation to a pelagic existence.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
Not a commercial species. ◆

Ornate ghost pipefish
Solenostomus paradoxus

FAMILY
Solenostomidae

TAXONOMY
Fistularia paradoxa Pallas, 1770, Indonesia.

OTHER COMMON NAMES
English: Harlequin ghost pipefish.

PHYSICAL CHARACTERISTICS
A morphologically remarkable fish. Body is very slender and straight, and head is very elongate, about one-third the total length. Mouth terminal, small, and upturned. Eyes round. First dorsal fin situated over pelvic fins, with five very long spines; second dorsal fin more posterior, with 17–23 rays. Anal fin opposite second dorsal, with 17–22 rays; pectoral fins inconspicuous, with 24 rays; pelvic fins located just anterior to the middle of the body, with seven rays; caudal fin large and spur-shaped when rays are extended. There are numerous dermal projections on snout, trunk, and tail. Body encased in 31–35 segmented bony plates. Coloration spectacular and ornate. Background color varies from white or semitransparent to black, with elaborate pattern of red, orange, white, or yellow spots, blotches, and stripes. Reaches some 4.7 in (12 cm).

DISTRIBUTION
Present in much of the Indo-West Pacific Ocean from the Red Sea and East Africa to the Marshall Islands and New Caledonia; occurs as far north as southern Japan and as far south as Australia.

HABITAT
Usually found in coral reef habitats (down to about 115 ft, or 35 m, in depth) among gorgonian corals, weeds, and algae or with crinoids over sand, along reef edges, or in sheltered coastal waters and estuaries.

BEHAVIOR
Typically a solitary species, but small groups of up to six individuals have been observed. This species is highly camouflaged, blending in very well with many different backgrounds. Young are mostly pelagic, but adults are more benthic; post-pelagic specimens are more transparent. Individuals may hover in a near vertical position when they are among gorgonians or other substrates.

FEEDING ECOLOGY AND DIET
Feeds on mysids, small shrimps, and other benthic crustaceans. Predators unknown but presumably larger reef-dwelling fishes.

REPRODUCTIVE BIOLOGY
In contrast to other syngnathoids, females carry the brood in a pouch that is formed by the enlarged pelvic fins (which are missing from other syngnathoids). Eggs are numerous, small, spherical, and somewhat transparent. Females fan the eggs by opening and closing their pelvic fins. Young are expelled from the pouch at birth. Other details concerning their reproduction are unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes kept as an aquarium fish; otherwise this species has no commercial value. ◆

Ringed pipefish
Doryrhamphus dactyliophorus

FAMILY
Syngnathidae

TAXONOMY
Syngnathus dactyliophorus Bleeker, 1853, Indonesia.

OTHER COMMON NAMES
English: Banded pipefish.

PHYSICAL CHARACTERISTICS
A very slender species, with both head and body on the same plane. Snout very slender, about one-eighth of the total length, with small upturned terminal mouth. Eyes round and relatively long. Single posterior dorsal fin, with 20–26 rays; small anal fin with four rays. Body has 15–17 bony rings, and tail has 18–22 bony rings. Caudal fin is round when expanded. Coloration composed of alternating black to reddish and yellow bars; caudal fin is white with a red circle. Reaches some 7.1 in (18 cm) in length.

DISTRIBUTION
This species is present throughout much of the Indo-West Pacific, in the Red Sea and East Africa to Samoa, and throughout Micronesia.

HABITAT
Inhabits a wide variety of coastal habitats, such as coral reefs, tide pools, lagoons, estuaries, sea grass meadows, and outer reef slopes. Frequently found in crevices and sheltered areas.

BEHAVIOR
A cryptic species, preferring to remain in caves or other shelters. Commonly seen in pairs, but occasionally large groups are formed. Young are pelagic and transparent (up to about 1.2 in, or 30 mm) and attain adult coloration only later, when they settle into a more benthic lifestyle.

FEEDING ECOLOGY AND DIET
Eats small crustaceans and may even clean larger fishes, such as morays, of small parasites. Consumed by larger fishes.

REPRODUCTIVE BIOLOGY
Males carry the eggs along their trunks ventrally. The eggs are small and spherical and reddish when fresh. The eggs are fertilized upon deposition on the male and hatch after a few weeks. Juveniles often are found in rock pools but typically are pelagic.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
A popular aquarium species, which has been reared in captivity. ◆

Lined seahorse
Hippocampus erectus

FAMILY
Syngnathidae

TAXONOMY
Hippocampus erectus Perry, 1810, West Indies.

OTHER COMMON NAMES
English: Seahorse.

PHYSICAL CHARACTERISTICS
Body erect and somewhat sinuous, with head at a right angle in relation to the trunk and tail. Snout moderately long, with small upturned mouth devoid of teeth. Eyes round. Two pairs of spines present behind the eyes on the head. Small pectoral fins with 14–17 rays; single posterior dorsal fin with 16–20 rays; small anal fin with three to four rays; no pelvic fins. Prehensile tail tapers into a slender stalk without a caudal fin. Trunk encased in 10–12 bony rings, each with four spines; tail has 32–38 rings. Coloration varies widely—background light brown, black, gray, or yellow (sometimes red) with various small blotches, stripes, and spots. Area around the eyes has small white stripes radiating from the eyes. Reaches 7.9 in (20 cm) in length.

DISTRIBUTION
Western Atlantic from Cape Cod (sometimes Nova Scotia as strays) to Uruguay. The extensive range suggests that the name *H. erectus* may be applied to a complex of closely related species.

HABITAT
Lined seahorses are found in habitats with heavy vegetation, such as seaweeds and sargassum, in shallow waters and waters as deep as 240 ft (73 m). Present also in bays, piers, beaches, salt marshes, oyster beds, and other environments in which vegetation and shelter are present. They are capable of tolerating great variations in temperature and salinity.

BEHAVIOR
Seahorses swim slowly, in a vertical position, by undulating the dorsal and pectoral fins and tend to cling with their prehensile tails to vegetation, gorgonian corals, and so forth. They produce sounds to communicate with each other. Younger individuals tend to be pelagic, sometimes swimming in groups.

FEEDING ECOLOGY AND DIET
Food consists mostly of small crustaceans, such as copepods, amphipods, and larvae. They employ pipette feeding, after a swift sucking action following a sudden upswing of the head. They are eaten by many species of bony fishes, including cod, bluefish, remoras, and spiny and smooth dogfishes.

REPRODUCTIVE BIOLOGY
Between 250 and 400 eggs are deposited in the male's brood pouch during courtship (the larger the female, the greater the number of eggs). Males develop brood pouches by about 3 in (7.5 cm) in length, and males with eggs are recorded at 3.5 in (9 cm). In courtship the male and female closely follow each other, and the male presents his pouch to the female's genital area. As eggs are being transferred from the female into the male's pouch, they both rise in the water and may change color. Breeding takes place in the summer or year-round in tropical climates. Females deposit a few eggs at a time repeatedly. The eggs develop in the brood pouch and may derive nourishment from secretions within the pouch. Eggs are pear-shaped and light orange in color and may contain one or more oil droplets. Eggs are incubated for 12–14 days in the pouch; there is no true larval period; miniature seahorses are expelled, measuring about 0.24 in (6 mm) in length. Their tails become prehensile after one day, and they become mature after three months.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
A common aquarium species whose commercialization requires monitoring. ◆

Leafy seadragon
Phycodurus eques

FAMILY
Syngnathidae

TAXONOMY
Phyllopteryx eques Günther, 1865, South Australia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
One of the most distinctive of all fishes, the leafy seadragon has numerous, complex leaflike dermal projections from the extremities of its head, trunk, and tail spines. Body is elongate, slender but somewhat sinuous, and encased in ringlike bony plates that extend as spines. The head is long, directed at almost a right angle in relation to the body, with a frontal bony projection and an extremely elongated snout. The mouth is upturned and terminal. Eyes round. Dorsal fin, which is poseterior, has 34–38 rays; pectoral fins have 19–21 rays; anal fin has four rays. Tail slender and prehensile, with leaflike dorsal projections. Pelvic and caudal fins, lateral line, and scales are absent. Coloration is greenish brown or yellow, with vertical stripes along the trunk. Head has slight mask and varying dark blotches on leaflike projections. Specimens in deeper waters (about 98 ft, or 30 m) tend to be more reddish. Reaches some 13.8 in (35 cm) in length.

DISTRIBUTION
Coastal regions of southern Australia from Western Australia (below Perth) to southern Victoria.

HABITAT
A marine species inhabiting shallow (down to about 98 ft, or 30 m), temperate waters, usually sheltered among algae and reefs but also found over sandy areas.

BEHAVIOR
A sluggish species, appearing to float aimlessly in kelp beds, protected by its elaborate camouflage. It may move rhythmically back and forth in a manner similar to algae being swept by currents. Adults may congregate in shallow bays in late winter to pair and mate. Divers can approach this species slowly. Cleaner shrimp and clingfish have been observed to "clean" parasites off leafy seadragons.

FEEDING ECOLOGY AND DIET
Feeds mostly on mysids and other crustaceans (e.g., shrimps and squad-lobsters). Predators unknown but presumably larger fishes.

REPRODUCTIVE BIOLOGY
Reproduction has been observed in the wild in this species. (Aquarium-bred specimens take some two years to reach adult size.) Females have greatly swollen trunks before spawning. Males carry a brood containing an estimated 250–300 elliptical eggs underneath their tails, posterior to the anal fins. The eggs, which measure 0.3 by 0.2 in (7 by 4 mm), are maintained in honeycomb-like egg pockets in the abdominal skin of the males. Pregnant males usually are seen in November or December. The tail of the male becomes swollen and turns bright yellow to indicate readiness to mate, at which time sperm are released into the abdominal region. The courtship ritual is similar to that of some pipefishes (in which the abdominal area is displayed to the mate, while the head is maintained in an upright position). The female deposits her eggs onto the abdominal region of the male, pushing them into place. At that point, egg pockets form on the male to fasten the eggs securely in place. Incubation takes about eight weeks. Males deposit hatchlings in a wide area, as hatching takes about one week. Hatchlings are advanced and settle on the bottom (at about 1.4 in, or 35 mm, in length), sometimes remaining in small groups and venturing into shallower water.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
An aquarium species that also attracts numerous recreational divers who want to see it up close (e.g., in Victoria Harbor, South Australia). This species cannot be collected off South Australia legally. It is somewhat difficult to maintain in aquaria, owing to its specialized feeding requirements, but aquarium-raised specimens may live for more than 10 years in captivity. Many aquarium specimens are bred in captivity. ◆

Weedy seadragon
Phyllopteryx teaniolatus

FAMILY
Syngnathidae

TAXONOMY
Syngnathus taeniolatus Lacepède, 1804, Bass Strait, Australia.

OTHER COMMON NAMES
English: Common seadragon.

PHYSICAL CHARACTERISTICS
Another remarkably distinct species. Body slender and elongate, highly arched between head and tail. Head at a slight angle to the body, with round eyes, very long snout, and small, upturned mouth. Encased in bony ringlike plates, many containing longer spines that have dermal leaflike flaps at the ends. Single dorsal fin situated posteriorly, with 27–34 rays; anal fin with four or five rays; pectorals with 20–23 rays. Tail prehensile, long, and slender, without a caudal fin; pelvic fins, lateral line, and scales absent. Coloration very ornate and somewhat varying—background usually reddish, with numerous closely packed yellow spots on head and body, bluish bars on sides of trunk and tail base, and darker dermal flaps. Reaches 18 in (46 cm) in length.

DISTRIBUTION
Southern Australian coast from central New South Wales to Rottnest Island (off Perth); also in Tasmania.

HABITAT
Typically found among algae, in kelp beds, and on rocky reefs, down to about 164 ft (50 m).

BEHAVIOR
A mostly solitary species, hovering among algae and sheltered rocky reefs, but also seen over sand. Individuals may move into deeper waters when food becomes less abundant.

FEEDING ECOLOGY AND DIET
As with the leafy seadragon, food principally consists of small crustaceans. Predators unknown but presumably larger fishes.

REPRODUCTIVE BIOLOGY
Many aspects of its reproduction are similar to that of the leafy seadragon. Males carry roughly equivalent numbers of eggs, which also are embedded in their skin. They usually have one brood per season, and mating begins from October to November. Young hatch after about two months, settling on the substrate. Hatchlings do not have the elongated snout of the adults, but it grows quickly; their elaborate dermal flaps are much smaller. Juveniles resemble adults by about 4.7 in (12 cm) in length.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
A popular aquarium species. Most specimens displayed are bred in captivity. They can live for more than 10 years in aquarium conditions. ◆

Resources

Books

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Marcelo Carvalho, PhD

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Synbranchiformes
(Swamp and spiny eels)

Class Actinopterygii
Order Synbranchiformes
Number of families 3

Photo: An African eel (*Mastacembelus* sp.) from Cameroon. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

No synbrachiform fossil is known. The Mastacembeloidei were removed from the Perciformes and added to the Synbranchiformes after a phylogenetic analysis by Johnson and Patterson. These authors consider the Synbranchiformes to be monophyletic and related to Mugiliformes, Atherinoformes, Gasterosteiformes, and Smegmamorformes.

There are two suborders: Synbranchoidei and Mastacembeloidei, or Opisthomi. The Synbranchoidei has one family, the Synbranchidae; four genera; and 15 species. The Mastacembeloidei has two families: Chaudhuriidae, with four genera and five species, and Mastacembelidae. The latter family is divided into two subfamilies, Mastacembelinae, with two genera and 25 species, and Afromastacembelinae, with two genera and 42 species). There are a total of 87 species.

Physical characteristics

These eel-like fishes range in size from 8 to 48 in (20–150 cm). Although they are eel-like, they are not related to true eels (Anguilliformes). The premaxillae are present as distinct bones. The gills are poorly developed, and their openings are usually single, small, and confluent across the breast. Oxygen is absorbed through the membranes of the throat or intestine. The dorsal and anal fins are low and continuous around the tail tip. Pelvic fins, if present, are small and located on the throat. Scales are either absent or very small. They lack a swim bladder.

Distribution

These fishes are distributed in tropical America, tropical Africa, southeastern and eastern Asia, East Indies, and Australia. The three families each have a somewhat different distribution: The Synbranchidae are found in Mexico, Central and South America, West Africa (Liberia), Asia, and the Indo-Australian Archipelago. The Mastacembelidae are found in Africa and through Syria to the Malay Archipelago and China. The Chaudhuriidae are found in northeastern India through Thailand to Korea (including parts of Malaysia and Borneo).

Habitat

They usually are found in swamps, caves, and sluggish fresh and brackish waters. When found in pools, they typically are associated with leaf litter and mats of fine tree roots along the banks. Swamp eels are capable of overland excursions, and some can live out of water for extended periods of time. Some species are burrowers. Four species are found exclusively in caves: *Monopterus eapeni* and *M. roseni* from India, *Ophisternon candidum* from Australia, and *O. infernale* from Mexico. One species, *O. bengalense*, commonly occurs in coastal areas of southeastern Asia.

Behavior

Some species are considered air-breathing fishes because of their ability to breathe by highly vascularized buccopharyngeal pouches (pharynx modified for breathing air). They usually are active only at night.

Feeding ecology and diet

They feed on benthic invertebrates, especially larvae, and fishes.

The zig-zag eel (*Mastacembelus armatus*) is found in the weedy stream beds of Southeast Asia, Sri Lanka, southern China, and Sumatra. (Photo by Hans Reinhard. Bruce Coleman, Inc. Reproduced by permission.)

An undescribed spiny eel (*Mastacembelus* sp.) from Southeast Asia. (Photo by Animals Animals ©Dani/Jeske. Reproduced by permission.)

Reproductive biology

At least some of the species of the family Synbranchidae, that is, *O. infernale*, are sexually dimorphic. Adult males grow a head hump, and males are larger than females. These fishes lay about 40 spherical eggs per clutch. The eggs measure between 0.05 and 0.06 in (1.2–1.5 mm) in diameter and have a pair of long filaments for adhesion to the substrate. Reproduction takes place during the wet season, which lasts for several months, during which females probably spawn more than once. Data acquired from studying juvenile growth and the length of representative individuals within a population suggests that they are a short-lived species that matures during the first year, with few individuals surviving to the second breeding season.

Conservation status

As of 2002, five species were listed by the IUCN as species of special concern: *Macrognathus aral* (the one-stripe spiny eel), *Monopterus boueti* (Liberian swamp eel), *Monopterus indicus* (Bombay swamp eel), and *Ophisternon candidum* (the blind cave eel) have been classified as Data Deficient, meaning that they require more study to determine their conservation status; *O. infernale* (blind swamp cave eel) is classified as Endangered.

Significance to humans

In some parts of Asia, swamp eels and one species of spiny eel, *Mastacembelus erythrotaenia*, are valued as food and sometimes are kept in ponds or rice fields. Except for a few mastacembelids, they are rarely seen in home aquaria.

1. Fire eel (*Mastacembelus erythrotaenia*); 2. Swamp eel (*Monopterus albus*); 3. Marbled swamp eel (*Synbranchus marmoratus*); 4. Blind cave eel (*Ophisternon candidum*). (Illustration by John Megahan)

Species accounts

Fire eel
Mastacembelus erythrotaenia

FAMILY
Mastacembelidae

TAXONOMY
Mastacembelus argus Bleeker, 1850, Moluccan Archipelago.

OTHER COMMON NAMES
German: Feueraal; Vietnamese: Cá chachlua.

PHYSICAL CHARACTERISTICS
Grows to 39.4 in (100 cm). Soft-rayed portions of the median fins and pectoral fin have a sharply defined white distal margin. The basal portion of the dorsal, anal, and caudal fins is dark and that of the pectoral fin is dark or has broad vertical bars. Head and anterior part of the body have longitudinal red and black bands; the rest of the body has red spots or elongated marks on a black background.

DISTRIBUTION
In Asia, from Thailand and Cambodia to Indonesia.

HABITAT
A large lowland floodplain species occurring in slow-moving rivers and inundated plains. Also found in streams and lakes.

BEHAVIOR
Under aquarium conditions individuals tend to spend daylight hours in a preferred shelter spot.

FEEDING ECOLOGY AND DIET
Feeds on benthic insect larvae, worms, and some plant material. Under aquarium conditions, specimens larger than 12 in (30 cm) in total length become predatory, hunting and eating smaller fishes. Vulnerable to larger fish, water snakes, crocodilians, and fish-eating birds as well as fishermen.

REPRODUCTIVE BIOLOGY
Nothing is know of the reproductive biology of this species. Other mastacembelids are egg scatterers, depositing a few eggs at a time in fine-leafed aquatic plants.

CONSERVATION STATUS
Not listed by the IUCN. This species has become rare in recent years due to human consumption and overfishing.

SIGNIFICANCE TO HUMANS
Often seen in the aquarium trade. Bred in fish farms in Bangkok. ◆

Swamp eel
Monopterus albus

FAMILY
Synbranchidae

TAXONOMY
Muraena alba Zouiev, 1793, type locality not specified.

OTHER COMMON NAMES
Cantonese: Wong sin; English: Rice (paddy field) eel; German: Ostasiatischer Kiemenschlitzaal; Japanese: Ta-unagi; Javanese: Welut; Khmer: Antong; Laotian: Pa lai; Malay: Belut; Thai: Pla lai; Vietnamese: Con lu'o'n, luon.

PHYSICAL CHARACTERISTICS
Grows to 39.4 in (100 cm). Eel-like body. It lacks scales and pectoral and pelvic fins. The dorsal, caudal, and anal fins are confluent and reduced to a skin fold. The gill openings merge into single slit underneath the head.

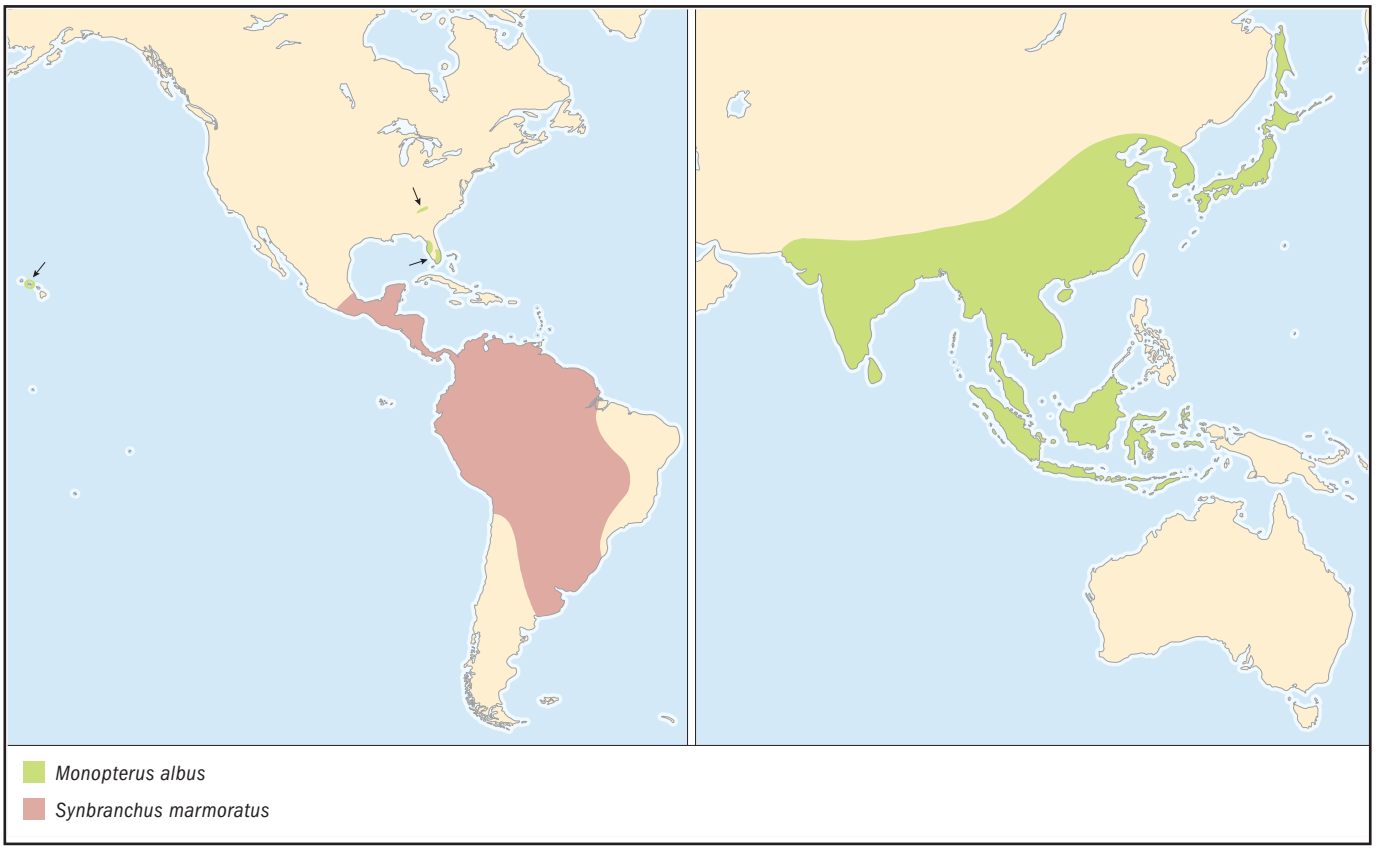
DISTRIBUTION
In India, China, Japan, Malaysia, and Indonesia. Probably also occurs in Bangladesh, Myanmar, and Thailand. Introduced populations in Florida, Georgia, and Hawaii in the United States.

HABITAT
It is a generalist that can be found in medium to large rivers, flooded fields, muddy ponds, swamps, canals and rice paddies; burrow in moist earth in dry season surviving for long periods without water.

BEHAVIOR
It burrows in moist earth at the beginning of the dry season, where it remains for long periods of time.

FEEDING ECOLOGY AND DIET
Feeds on detritus, plants, and small animals. Vulnerable to crocodilians, otters, and fish-eating birds.

REPRODUCTIVE BIOLOGY
External fertilization. Builds a bubble nest at the surface of the water near the shoreline. It is not known whether care is afforded to the eggs and fry. Spawning takes place in shallow



water. After spending part of their lives as females, some individuals undergo sex reversal, and change into males. Sex reversal is completed within eight to 30 weeks. All larger individuals are males.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Marketed fresh because of the good quality of its flesh. Stays alive for long periods of time as long as the skin is kept moist. Occasionally sold as an aquarium fish. ◆

Blind cave eel
Ophisternon candidum

FAMILY
Synbranchidae

TAXONOMY
Anommatophasma candidum Mees, 1962, Yardie Creek Station, North West Cape, Western Australia.

OTHER COMMON NAMES
Spanish: Anguila ciega.

PHYSICAL CHARACTERISTICS
Grows to 15.8 in (40 cm). These fishes have a very elongated, eel-like, and roundish body with no fins, except for a thin, rayless fin fold near and around the tip of the tail. The lateral line system is distinct and continues to near the tip of the tail. It is whitish in coloration, lacks externally visible eyes, and is scaleless.

DISTRIBUTION
This species used to be found in 11 locations (two now destroyed) in the western and northeastern coastal plain of the Cape Range Peninsula of Australia.

HABITAT
Inhabits wells, sinkholes, and caves and possibly also occurs in aquifers.

BEHAVIOR
No information is available.

FEEDING ECOLOGY AND DIET
This species feeds on invertebrates, both hypogean and epigean, that accidentally fall into its habitat. Due to its habitat, it is not subject to predation.

REPRODUCTIVE BIOLOGY
External fertilization. No additional information is available.

CONSERVATION STATUS
Listed as Data Deficient by the IUCN.

SIGNIFICANCE TO HUMANS
Of ecological and scientific interest only. ◆

Marbled swamp eel
Synbranchus marmoratus

FAMILY
Synbranchidae

TAXONOMY
Synbranchus marmoratus Bloch, 1795, Rio Negro, Brazil.

OTHER COMMON NAMES
English: Swamp eel; French: Anguille; German: Amerikanischer; Spanish: Anguila.

PHYSICAL CHARACTERISTICS
Grows to 50.1 in (150 cm). It has a long and cylindrical body, lacking pectoral and ventral fins and with vestigial dorsal and anal fins. The species has small eyes.

DISTRIBUTION
From Mexico to Central Argentina.

HABITAT
This species inhabits fresh and brackish waters in a variety of habitats, including streams, canals, drains, ponds, and rice fields. It can be seen in both clear and murky waters.

BEHAVIOR
This is a nocturnal fish usually found at the edge of the water. It can travel over land for considerable distances. It also burrows, especially during the dry season. During that time its metabolism is reduced considerably, but it still may flee if disturbed. After the first rains, it returns to larger bodies of water.

FEEDING ECOLOGY AND DIET
They feed on fish and invertebrates and are considered aggressive predators. They are vulnerable to crocodilians and fish-eating birds.

REPRODUCTIVE BIOLOGY
This is a species characterized by two unusual reproductive methods. In the first, many individuals undergo sequential hermaphroditism, where some fish function first as females and then as males, called terminal males. This condition is called protogy, and species that have such individuals are called protogynous. Those individuals that are males from the beginning are called primary males. Some individuals remain juvenile females, a condition termed diandric. They have external fertilization and show some level of genetic variability, which is consistent with the fact that this is a generalist species with a broad distribution in the New World. No specific seasonal reproductive data or parental care information has been published.

CONSERVATION STATUS
Because of its broad distribution, it is not considered threatened. Owing to its burrowing behavior, however, it may be missed in many faunal surveys.

SIGNIFICANCE TO HUMANS
Is not infrequent in public aquaria although it does not make a good exhibit because of its burrowing behavior. Because of its size it is difficult to keep in home aquaria. ◆

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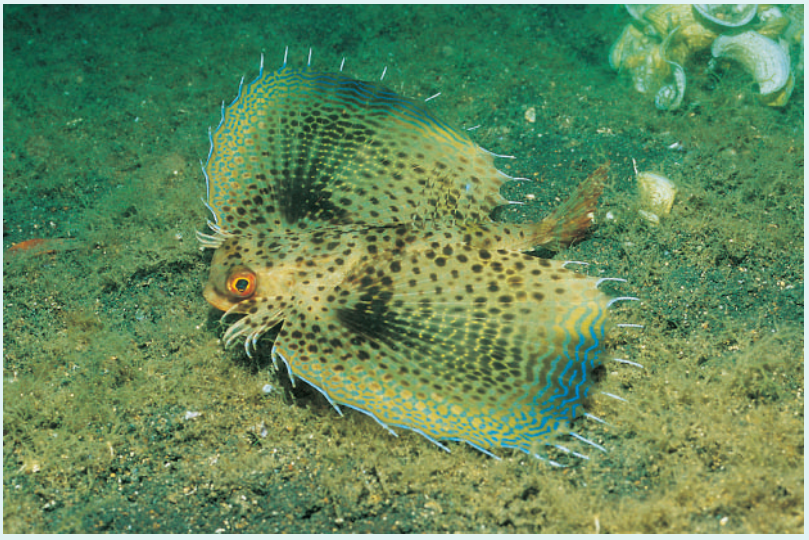
Aldemaro Romero, PhD

Scorpaeniformes I
(Gurnards and flatheads)

Class Actinopterygii
Order Scorpaeniformes
Number of families 4

Photo: An Oriental helmet gurnard (*Dactyloptena orientalis*) sleeping on the lava sand of the Lembeh Straits of Sulawesi Island, Indonesia. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)



Evolution and systematics

The two suborders that comprise this chapter, the flatheads (Platycephaloidei) and flying gurnards (Dactylopteroidei) are mail-cheeked fishes (order Scorpaeniformes). This old group (first recognized in 1829), composed of approximately 1,400 species, is united by the presence of the suborbital stay. The suborbital stay is a bony strut that connects the bones under the eye with the front of the gill cover. Some authors have suggested that the suborbital stay in the flying gurnards evolved independently from the remainder of the scorpaeniform fishes. These authors place the flying gurnards in their own order (Dactylopteriformes).

In 1758 the father of binomial nomenclature, Carl Linnaeus, was the first naturalist to describe species of both the flying gurnards and the flatheads. Since the time of Linnaeus, six additional flying gurnards and 86 additional platycephaloids have been described. The seven flying gurnards are now classified into two genera (*Dactylopterus* in the Atlantic and *Dactyloptena* in the Indo-Pacific). The 88 platycephaloids have been classified variously into three to seven families, depending on the researcher. For the purposes of this review, the Platycephaloidei are split into three families: the flatheads (Platycephalidae, 64 species), the ghost flatheads (Hoplichthyidae, 11 species), and the deepwater flatheads (Bembridae, 11 species). At this time, there is considerable debate about the placement and classification of both of these suborders, so the classification follows Joseph Nelson's 1994 book, *Fishes of the World.*

Traditionally, the flying gurnards have been allied with the sea robins (Triglidae and Peristediidae), because both groups share enlarged pectoral fins and free pectoral rays, which these fishes use like legs to "walk" on the seafloor. Recently, researchers have suggested that the suborbital stay in flying gurnards evolved independently of the strut found in other mail-cheeked fishes. These ichthyologists have suggested that flying gurnards are related to the seahorses and their relatives (Sygnathoidei) or to the tilefishes (Malacanthidae). Because of these different views, the interrelationships of the flying gurnards remain unclear, and they are treated here as scorpaeniforms, pending resolution of their placement.

The placement of the flatheads and their relatives is not clear either. Historically, the three flathead families have been united because of their elongate bodies and depressed or "flattened" heads; hence their common name. Recent work by Hisashi Imamura has suggested that the sea robins and their relatives (Triglidae and Peristediidae) may have evolved from a flathead relative, suggesting that the sea robins should be placed in the Platycephaloidei. Clearly, further work using both morphological and DNA sequence data will shed light on the interrelationships and intrarelationships of the flatheads and their allies.

At more than 50 million years old, the enigmatic *Pterygocephalus paradoxus* from the Monte Bolca formation in Italy may be the oldest known flying gurnard, but the fossil *Prevolitans faedoensis* from Eocene deposits in northern Italy is the oldest clearly identifiable flying gurnard. Flatheads first appear in the fossil record with an Eocene otolith (ear stone) record identified as *Platycephalus janeti* from France. Whole fossilized skeletal specimens of *Platycephalus* date to the early Miocene in Tasmania.

Physical characteristics

Flying gurnards are one of the most recognizable of all spiny-rayed fishes because of their large heads, greatly developed winglike pectoral fins, and free pectoral rays. Their bodies are covered with ctenoid scales. They have a very

characteristic "helmet-like" skull with a strong preopercular spine that gives them their other common name (helmet gurnards). Dactylopterids have a short snout with a subterminal mouth. Their jaws are filled with small, conical teeth. Flying gurnards have two dorsal fins separated by a deep notch, which typically have a couple of free dorsal spines detached from and preceding the first dorsal fin. As was found in the flatheads, sculpins (Cottoidei), and some sea robins, the dactylopterids lack true anal spines.

Typically, flying gurnards lie on the seafloor with their pectoral wings folded against the body. When dactylopterids have their wings folded, they are well camouflaged on the seafloor because of their dusky red and drab white, brown, and black markings. When startled, however, flying gurnards quickly spread their brightly colored pectoral fins (covered with bluish and whitish spots, for example) to distract would-be predators and make their quick escape. Flying gurnards can reach lengths of up to 15.7 in (40 cm).

Flatheads are recognized easily by their elongate bodies with depressed, broad heads. They typically are covered with ctenoid scales, except for their lower flanks and ventral surfaces, which often are covered by cycloid scales. The ghost flatheads lack scales, but their dorsal surface is overlaid with spiny, bony plates. All flatheads and their allies have large eyes placed close together high on their heads. The eyes of platycephalids often are covered with highly ornamented eye flaps. All platycephaloid heads are overlaid with bony or spiny ridges. These ridges are particularly well developed in the ghost flatheads. Platycephaloid jaws are filled with numerous bands of small, conical teeth, but *Ratabulus megacephalus* has strong canine teeth. Flatheads have two dorsal fins, the first with true spines. Bembrids and hoplichthyids usually have a single anal spine, but true anal spines are lacking in platycephalids. Most flatheads are dark dorsally and pale ventrally. The dark colors are various shades of brown, black, or gray, but the more colorful taxa can be red, purple, and green. The deepwater flatheads tend to be red, orange, and light brown, and the ghost flatheads are typically yellow, pink, or brown. Ghost flatheads and bembrids usually are smaller (11.8–15.7 in, or 30–40 cm) than the larger platycephalids (up to 27.6 in, or 70 cm).

Distribution

The flying gurnards are distributed in tropical and temperate waters in the Indo-Pacific and Atlantic Oceans. They usually are found in nearshore environments, whereas larval and juvenile dactylopterids are found in open ocean (pelagic) environments, where they can be collected at night using attracting lights and handheld dipnets.

The flatheads and relatives are distributed in the tropical and temperate waters of the Indo-Pacific, Mediterranean, and eastern Atlantic. Platycephalids are found on the continental shelf at depths to 984 ft (300 m), but most are found at less than 330 ft (100 m). Bembrids also live on the continental shelf, but they typically are taken at deeper depths (hence their common name, deepwater flatheads), down to 1,900 ft (581 m). Although there are significantly fewer ghost flatheads, they have a much wider depth distribution, ranging from 200 to 4,900 ft (60–1,500 m).

Habitat

Both the flying gurnards and flatheads typically are found on the continental shelf in mud or sandy bottoms. There is also a second group of flathead species commonly found in rocky shore habitats and coral reefs.

Behavior

Although the common name of the dactylopterids suggests that these fishes can fly, they cannot; only the true flying fishes (Exocoetidae) are capable of flight. It is for this reason that many authors have suggested that the common name be changed to helmet gurnards. It is likely that the giant pectoral fins are spread quickly, to scare "would-be" predators, to communicate with conspecifics, or for controlled gliding over the seafloor for prey. Dactylopterids can produce sound by stridulating the hyomandibular bone. Flatheads and their allies are typical "lie and wait" predators that spend most of their time buried completely or partially in the sand or mud.

Feeding ecology and diet

"Walking" quickly over the seafloor by moving their pelvic fins and their short pectoral fin rays alternately, flying gurnards sift through the sandy bottom in search of the next crustacean or fish, which they stir up and capture.

Lying on the seafloor buried partially beneath the sand, flatheads wait to ambush the next crab, fish, or shrimp that swims by. Like chameleons and flounders, flatheads have developed the ability to mimic the color pattern of the substrate on which they are lying. Platycephaloids are modified further for this "lie and wait" feeding strategy by specializations of the respiratory and pelvic structures that allow them to breathe while they are buried and to accommodate larger prey items. These numerous modifications make flatheads one of the premier ambush predators in the Indo-West Pacific.

Flatheads and gurnards are preyed upon by mammals (e.g. humans) and numerous species of larger, predatory fishes.

Reproductive biology

Very little is known about the reproductive biology of the flatheads and flying gurnards. All families produce pelagic, nonadhesive eggs. Japanese researchers have shown that some flatheads (e.g., *Suggrundus meerdervoortii* and *Cociella crocodila*) begin life as males and undergo sex reversal to become females as they grow older.

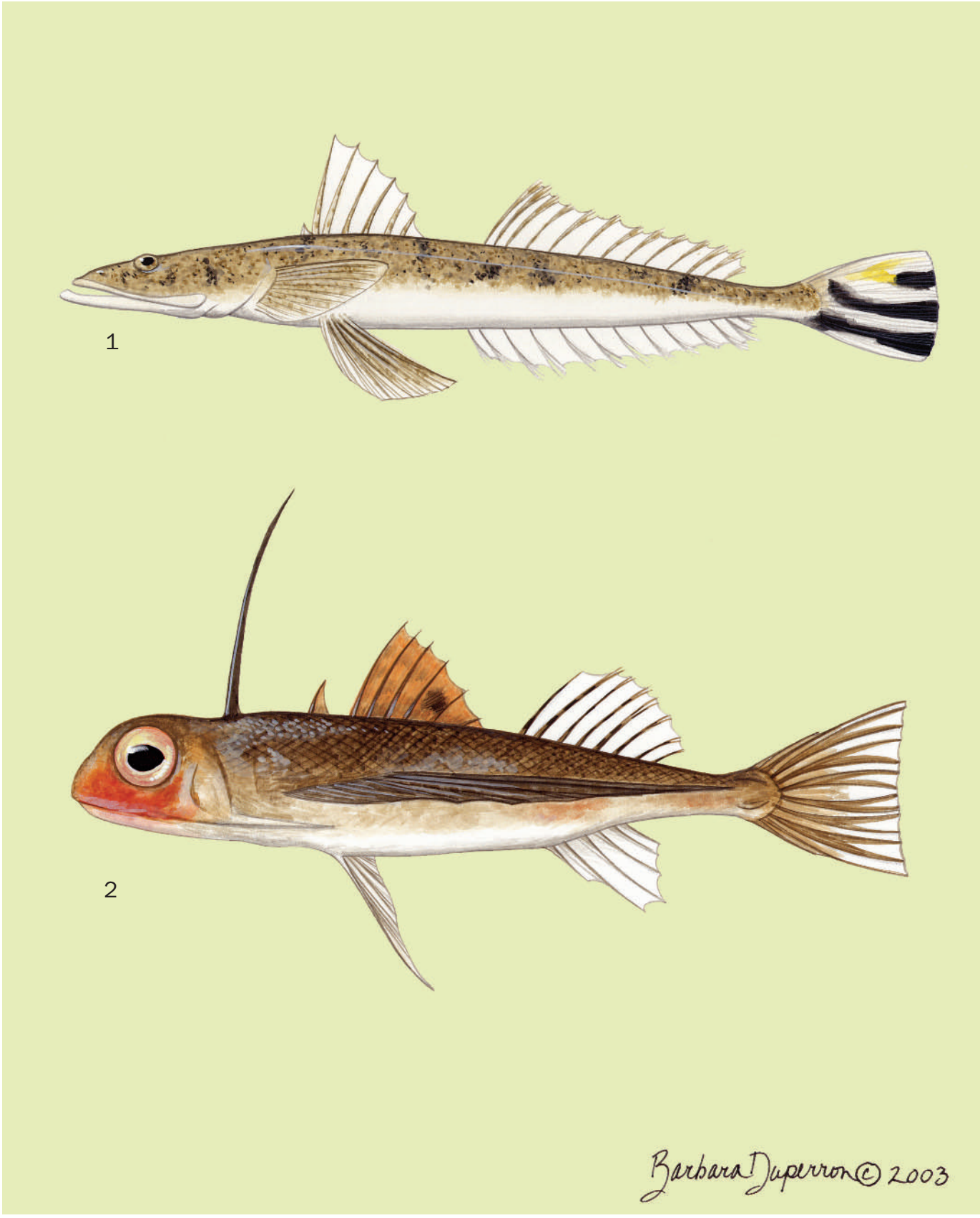
Conservation status

At the present time, no platycephaloid or dactylopterid species are included on the IUCN's Red List, although many species are quite rare.

Significance to humans

Of the four families, only the platycephalids are a commercially important food source for humans. Flying gurnards occasionally are fished for human consumption, but the fisheries are primarily for personal use. Bembrids and hoplichthyids do not have commercial fisheries, although the flesh of the ghost flatheads is supposed to be of good quality.

Although none of these fishes is as common in the aquarium trade as their lionfish or scorpionfish relatives, both dactylopterids (e.g., *Dactyloptena orientalis* and *Dactylopterus volitans*) and the crocodilefish (*Cymbacephalus beauforti*) occasionally are available in the aquarium trade.



1. Indian flathead (*Platycephalus indicus*); 2. Oriental helmet gurnard (*Dactyloptena orientalis*). (Illustration by Barbara Duperron)

Species accounts

Oriental helmet gurnard
Dactyloptena orientalis

FAMILY
Dactylopteridae

TAXONOMY
Dactyloptena orientalis Cuvier, 1829, Red Sea.

OTHER COMMON NAMES
French: Grondin volant oriental; Spanish: Alón oriental; Japanese: Semihôbô.

PHYSICAL CHARACTERISTICS
Grows to 15.7 in (40 cm) maximum length. Body moderately elongate with large, heavily armored head and greatly expanded winglike pectoral fins. Head broad and blunt, with large eyes and a small subterminal mouth. A unique fish that is gray to light brown, with dark brown and black spots on its back and upper sides. The elongate first dorsal spine is well separated from the second dorsal spine and the remainder of the first dorsal fin. The enlarged pectoral fins also are spotted, with striking blue wavy lines near the margins of the fins.

DISTRIBUTION
This widely distributed species ranges from the western Indian Ocean and Red Sea east to the Polynesian and Hawaiian Islands.

HABITAT
A benthic species that spends most of its time on sandy bottoms.

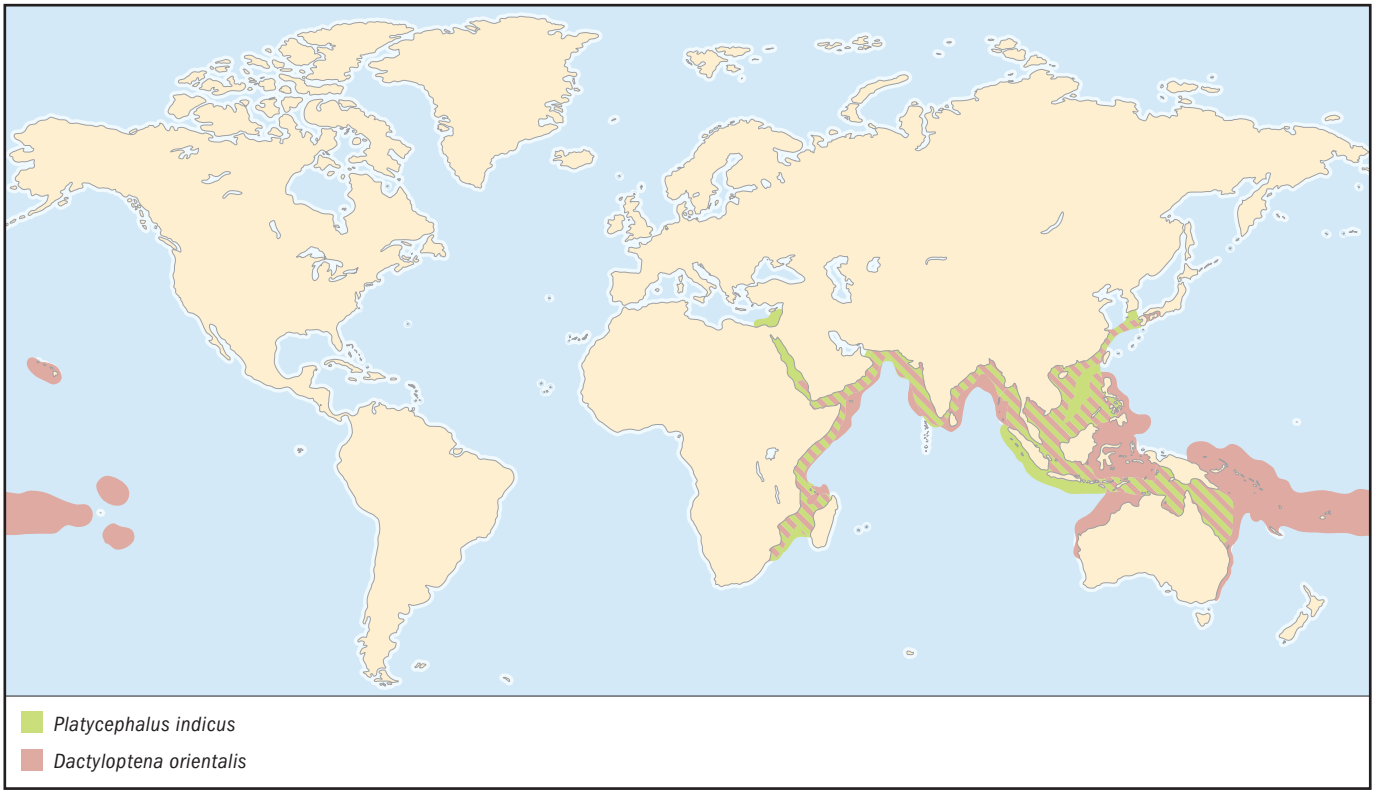
BEHAVIOR
A bottom-dwelling fish that quickly expands its pectoral fins as a defensive behavior.

FEEDING ECOLOGY AND DIET
Feeds primarily on benthic crustaceans, clams, and fishes that it stirs up as it "walks" along the seafloor.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of the Oriental flying gurnards in the wild, although one aquarium wholesaler has started offering aquacultured flying gurnards to aquarists.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A specialty item in the aquarium trade and incidentally fished in the Indo-Pacific, but not commercially collected for consumption. ◆



Indian flathead

Platycephalus indicus

FAMILY
Platycephalidae

TAXONOMY
Platycephalus indicus Linneaus, 1758, Asia.

OTHER COMMON NAMES
English: Bartail flathead; French: Platycéphale des Indes; Spanish: Chato índico; Japanese: Kochi.

PHYSICAL CHARACTERISTICS
Grows to 39.4 in (100 cm) in maximum length. Characteristic flattened head with various spinous ridges. Vomerine and palatine teeth are canine-like, with broad bands of villiform teeth in jaws. The two dorsal fins are well separated, with an isolated short spine before the first dorsal fin. Body covered with small ctenoid scales. Brownish coloration with eight or nine obscure dusky bands over the back. All fins, except the caudal fin, are covered with dusky spots on the rays. Caudal fin has a median longitudinal black band below and two oblique bands above.

DISTRIBUTION
Known from Israel and Egypt (entered the Mediterranean through the Suez Canal), eastern Africa, India, Indonesia, China, southern Japan, the Philippines, and Western Australia.

HABITAT
Typically found on rocky and soft bottoms at depths from 33 to 656 ft (10 to 200 m).

BEHAVIOR
A bottom-dwelling fish that spends most of its time buried beneath the sand or among rocks waiting to ambush its next prey.

FEEDING ECOLOGY AND DIET
Feeds primarily on benthic crustaceans and small fishes.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of the Indian flathead.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally harvested, but not a fish of great commercial importance. ◆

Resources

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William Leo Smith, MS

Scorpaeniformes II
(*Scorpionfishes and relatives*)

Class Actinopterygii
Order Scorpaeniformes
Number of families 14

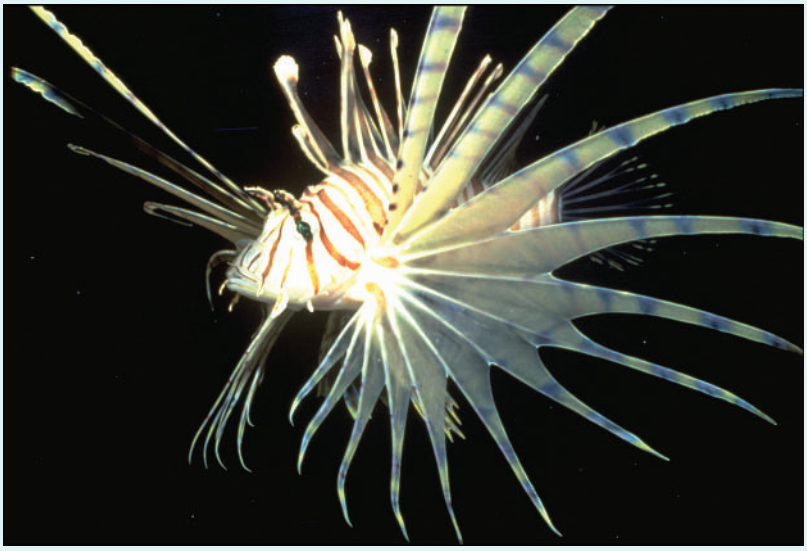


Photo: A red lionfish (*Pterois volitans*) in the Coral Sea. The lionfish can give vemonous stings from its pelvic, dorsal, and anal spines. (Photo by JLM Visuals. Reproduced by permission.)

Evolution and systematics

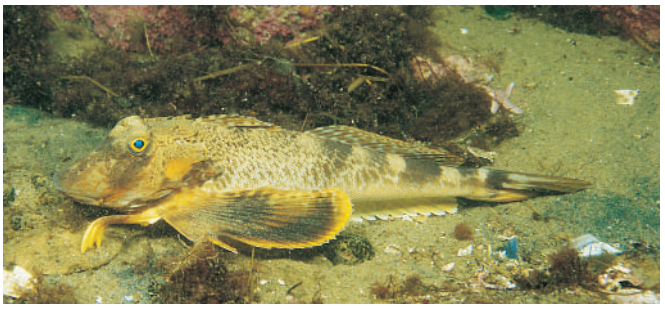
The approximately 1,400 species of mail-cheeked fishes (order Scorpaeniformes), first grouped together by the naturalist Georges Cuvier, are united because they share a single remarkable feature. This feature, the suborbital stay, is a bony strut that connects the bones under the eye with the front of the gill cover. This character is found in all scorpaeniforms except the Australian prowfishes (Pataecidae). The gapers (Champsodontidae) are sometimes included in the Scorpaeniformes, but here are included in the Trachinoidei chapter.

This chapter covers the suborder Scorpaenoidei. Because scorpaenoids are the dominant group of venomous fishes, they have one of the oldest and best-documented natural histories (especially in terms of venomology), dating back almost 2,400 years. Even with this detailed historical record, the classification and taxonomy of the Scorpaenoidei remain some of the most difficult of all fish orders. The composition of the group presented here follows Joseph Nelson's 1994 book, *Fishes of the World*. The classification of the scorpionfishes and sea robins presented here is updated from Nelson's book and follows more recent studies.

The Scorpaenoidei is divided into two groups: the sea robins (composed of either one or two families) and the scorpionfishes and their relatives (composed of seven to thirteen families). Following Hisashi Imamura's 1996 analysis, there are two families of sea robins: the sea robins (Triglidae, about 110 species) and the armored sea robins (Peristediidae, about 40 species). Following Minoru Ishida's 1994 analysis and recent work by Randall Mooi and David Johnson, there are 12 families of scorpionfishes: longfinned waspfishes (Apistidae, three species), velvetfishes (Aploactinidae, about 40 species), orbicular velvetfishes (Caracanthidae, four species), pigfishes (Congiopodidae, nine species), red velvetfish (Gnathanacanthidae, one species), gurnard perches (Neosebastidae, 12 species), prowfishes (Pataecidae, three species), scorpionfishes (Scorpaenidae, some 200 species), rockfishes (Sebastidae, roughly 125 species), midwater scorpionfishes (Setarchidae, five species), stonefishes (Synanceiidae, about 35 species), and waspfishes (Tetrarogidae, about 40 species).

Traditionally, the scorpionfishes and their relatives have been grouped with the sea robins. Recent work suggests that the sea robins might be related more closely to the flatheads (Platycephaloidei); this hypothesis needs further testing. Generally, it is agreed upon that the Platycephaloidei and the Scorpaenoidei make up the "scorpaenoid lineage." All species in this lineage are united by the presence of an opercular spine (the largest bone that makes up the gill cover) that projects beyond the subopercle (the posterior margin of the gill cover) and a derived gas bladder muscle configuration. The Scorpaenoidei usually is treated as the most primitive group of scorpaeniforms, with the rockfishes (Sebastidae) representing the basic body form. Some researchers have argued that the rockfishes have numerous derived features, including live birth and modified gas bladder muscles, making them a poor choice for a primitive form. Because of these disagreements and the countless classifications that exist, a worldwide revision of the group is needed. In particular, an analysis of morphological and DNA sequence data is needed to resolve the remaining questions in scorpaenoid phylogeny and classification.

Regardless of the classification used, there are no known characters that unite all members of the Scorpaenoidei with or without the sea robins and relatives (Triglidae and Peristediidae). The scorpionfish and relatives clade can be broken into two groups. The first group is composed of the taxa that have the first and/or second dorsal spines and supports



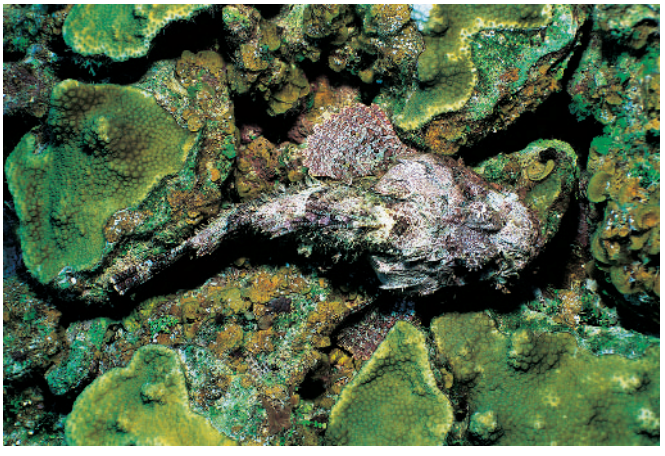
A northern sea robin (*Prionotus carolinus*) "walking" on its fins in the Gulf of Maine. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

articulating with the skull; this includes the families Aploactinidae, Congiopodidae, Gnathanacanthidae, Pataecidae, Synanceiidae, and Tetrarogidae. The remaining seven families have the traditional arrangement where the dorsal fin begins beyond the posterior margin of the skull. Recent work has suggested that the Australian prowfishes (Pataecidae) might not be related to the other scorpionfishes.

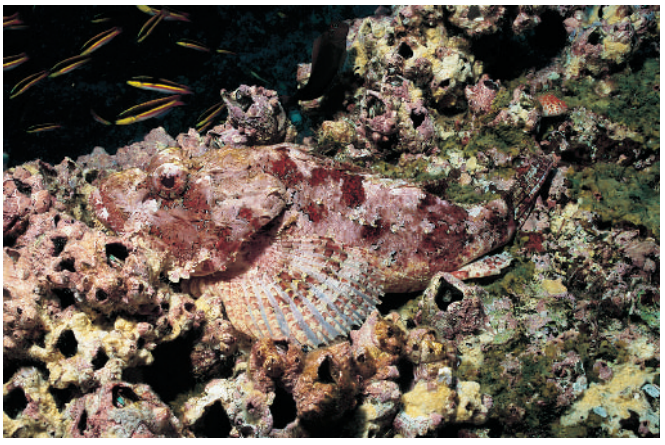
The scorpionfishes and their relatives first appear in the fossil record with an Eocene otolith (ear stone) record identified as *Scorpaenoideorum prominens* from the London Clay Formation in southern England. Another scorpaenoid fossil from the Miocene is the earliest scorpaenoid known from skeletal remains. This specimen is a fossil stonefish, *Eosynanceja brabantica*, from Belgium, which is known from a handful of bones, including portions of the jaw, cheek, and vertebral column.

Physical characteristics

Most sea robins and armored sea robins are medium-sized fishes, up to 15.7 in (40 cm). Their most conspicuous characters are their greatly expanded pectoral fins and a head that is completely encased in bony plates. The armored sea robins, as their name suggests, take this protection one step further. Their entire body is covered with spine-bearing plates. Like



A spotted scorpionfish (*Scorpaena plumieri*) is well camouflaged in the coral of the Caribbean. (Photo by Animals Animals ©Franklin J. Viola. Reproduced by permission.)



A Pacific spotted scorpionfish (*Scorpaena mystes*) mimicking the colorful sponges near Darwin Island, Galápagos Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

the flying gurnards (Dactylopteridae) and some stonefishes (Synanceiidae), both families have detached, fingerlike pectoral rays that they use as tactile and chemoreceptive organs. These elongate, free rays also are used for "walking" along the seafloor in search of prey.

The scorpionfishes and their relatives have a wide range of sizes, from the smallest velvetfishes at 0.8–1.2 in (2–3 cm) to the largest rockfishes at about 39.4 in (about 100 cm). Their diversity of sizes is matched by their diversity in body forms, with only numerous sharp spines being common to all species, although most species could be described as "bass-like." Scorpaenoids fall into one of two categories. The first group is composed of the brightly colored, highly venomous species (e.g., the lionfishes) that hover around coral reefs displaying their warning coloration. The second category is made up of the cryptic species. These species tend to be dominated by colors that mimic their surroundings. Additionally, these species are covered with numerous cirri, fleshy appendages, spines, and ridges; these appendages provide additional camouflage.

Distribution

The Scorpaenoidei has a worldwide distribution in tropical and temperate marine waters. Most scorpaenoids (e.g., Scorpaenidae, Synanceiidae, Aploactinidae, and Tetrarogidae) are found primarily in the tropical Indo-Pacific. One tetrarogid, the bullrout (*Notesthes robusta*) from eastern Australia, is the only freshwater scorpaenoid. The other center of diversity for the scorpaenoids is the northern Pacific Ocean, which is dominated by the more than 80 species of rockfishes (Sebastidae).

Habitat

Almost all scorpaenoids are benthic predators that are found in rocky, sea grass, or coral habitats. Basically, scorpionfishes can be found in any topographically complex environment, where they can use their cryptic coloration and

appendages to hide. Typically, sea robins, which are not as cryptic, are more common on sandy, rocky, or muddy habitats. Finally, the deep-water or midwater setarchids and armored gurnards are benthic species that are found at depths up to 6,562 ft (2,000 m), although most species are found at less than 2,297 ft (700 m).

Behavior

There are few generalizations that can be made about the behavior of scorpaenoid fishes. Most scorpaenoids are territorial and lead solitary lives, except for the formation of mating aggregations. Scorpaenoids are masters of disguise. Many species have cryptic coloration; numerous leaflike appendages, or cirri; epibiotic growth; and bony ridges that give the appearance of rocks. Other scorpaenoid species have specialized pectoral fins that allow them to bury themselves in the sand. All of these features help scorpaenoids blend into their environment as they lie waiting for prey.

In addition to their camouflage and mimicry, scorpaenoids are protected in their environment by their pungent, venomous dorsal spines. Almost all scorpaenoids, except such groups as prowfishes (Pataecidae) and sea robins and their allies (Triglidae and Peristediidae), have venom glands associated with the fin spines. The venom from these glands has both neurotoxic (affecting the nervous system) and hemotoxic (affecting the blood vessels) action, which has led to numerous human fatalities and given these species their infamous reputation. The venom of the colder-water species (e.g., the rockfishes, Sebastidae) generally has less severe effects, and that of the stonefishes (Synanceiidae) and lionfishes (*Pterois*) is most deadly. The stonefishes, in particular, have devised a particularly dastardly venom apparatus that has a hollowed-out dorsal spine with muscular control, which basically gives them a hypodermic needle to inject their deadly venom. Fortunately, we have learned that the effects of the venom are minimized if the affected area is soaked in very hot (not boiling) water to help denature the proteins; additionally, topical treatment with stonefish antivenoms limits the damage.

A red lionfish (*Pterois volitans*) eating a zebra turkeyfish (*Dendrochirus zebra*). (Photo by Tom McHugh/Steinhart Aquarium/Photo Researchers, Inc. Reproduced by permission.)

A tub gurnard (*Chelidonichthys lucerna*) on top of a European plaice (*Pleuronectes platessa*). (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Almost all scorpaenoids are benthic predators that feed primarily on crustaceans and smaller fishes. Most species are typical lie-and-wait predators that use their highly camouflaged bodies and burst speed to capture prey. The sea robins (Triglidae) have excised pectoral rays that are chemoreceptive. These fishes run these fingerlike rays through the sand or mud to locate prey as they walk along the seafloor. Adult scorpaenoid fishes are rarely preyed upon because of their powerful venom, but venomous juveniles and less venomous species (e.g., rockfishes) are preyed upon by larger fishes, humans, and pinnipeds (e.g., California sea lion).

Reproductive biology

There are numerous reproductive modes in the Scorpaenoidei. All species are iteroparous (having more than one spawning event per lifetime) and have many sexual partners (at least the males). One of the most interesting scorpaenoid reproductive strategies is live birth, which is found in some

The face of a tub gurnard (*Chelidonichthys lucerna*) near Brittany, France, in the Atlantic Ocean. (Photo by Jeff Rtman/Photo Researchers, Inc. Reproduced by permission.)

rockfishes (Sebastidae). The live-born *Sebastes* embryos are interesting, because they derive nutrients both from the yolk sac and directly from the mother. A possibly related reproductive strategy is used by many scorpaenoids (e.g., *Pterois* and *Sebastolobus*). In this strategy, the male inseminates the female, and then the female extrudes the fertilized eggs in a gelatinous mass that floats at the surface. There are many scorpaenoid species that are typical broadcast spawners with planktonic larvae, for example, sea robins (Triglidae) and pigfishes (Congiopodidae). Last, there are two scorpaenoid families whose reproductive biology is unknown—orbicular velvetfishes (Caracanthidae) and velvetfishes (Aploactinidae).

Conservation status

At the present time, there are four scorpaenoids listed by the IUCN. First is the deepwater jack, *Pontinus nigropunctatus*, from Saint Helena, which is considered Vulnerable. The redfish, *Sebastes fasciatus*, from the northwest Atlantic and *Sebastolobus alascanus* from the northeast Pacific, are considered Endangered. Finally, the bocaccio, *Sebastes paucispinis*, from the northeast Pacific is considered Critically Endangered. These species, except for the deepwater jack, have been reduced to critical levels because of the pressures of overfishing. A recent report suggests that another eleven species of rockfishes (Sebastidae) also should be given protected status in North America because of continually declining numbers due to overfishing.

Significance to humans

Despite their venomous nature, many scorpaenoids support important commercial and recreational fisheries worldwide. The rockfish fishery in the northern Pacific and Atlantic is one of the best known. Unfortunately, many *Sebastes* species have been overfished. This exploitation is due to numerous factors, including life history traits, oceanography, and the difficulty in identifying larval species, which interferes with accurate population management. Another interesting scorpaenoid fishery is the commercial harvesting of the highly venomous stonefish, *Synanceia verrucosa*, for live fish markets in Hong Kong. This fishery has been so successful that there is serious discussion about aquaculturing the highly venomous stonefish species.

The lionfishes (*Pterois* and *Dendrochirus*) make up one of the dominant groups of fishes in the marine aquarium trade. These fishes are not bred in captivity; all are collected from the wild. In addition to the large number of lionfishes that are collected annually, many other scorpaenoids are collected occasionally for the aquarium trade (e.g., the weedy scorpionfish (*Rhinopias*), the sea robin (*Prionotus*), and the bearded ghoul (*Inimicus*).

1. Bearded ghoul (*Inimicus didactylus*); 2. Ocellated waspfish (*Apistus carinatus*); 3. Crested scorpionfish (*Ptarmus jubatus*); 4. Striped sea robin (*Prionotus evolans*); 5. Deepwater scorpionfish (*Setarches guentheri*); 6. South American pigfish (*Congiopodus peruvianus*); 7. Reef stonefish (*Synanceia verrucosa*); 8. Cockatoo waspfish (*Ablabys taenianotus*). (Illustration by Jonathan Higgins)

1. Belalang (*Gargariscus prionocephalus*); 2. Red lionfish (*Pterois volitans*); 3. California scorpionfish (*Scorpaena guttata*); 4. Red indianfish (*Pataecus fronto*); 5. Merlet's scorpionfish (*Rhinopias aphanes*); 6. Bocaccio (*Sebastes paucispinis*); 7. Red gurnard (*Chelidonichthys spinosus*); 8. Spotted coral croucher (*Caracanthus maculatus*). (Illustration by Jonathan Higgins)

Species accounts

Ocellated waspfish
Apistus carinatus

FAMILY
Apistidae

TAXONOMY
Apistus carinatus Bloch and Schneider, 1801, Tranquebar, India.

OTHER COMMON NAMES
English: Bearded waspfish; French: Rascasse ocellée; Spanish: Rascacio ocelado; Japanese: Hachi.

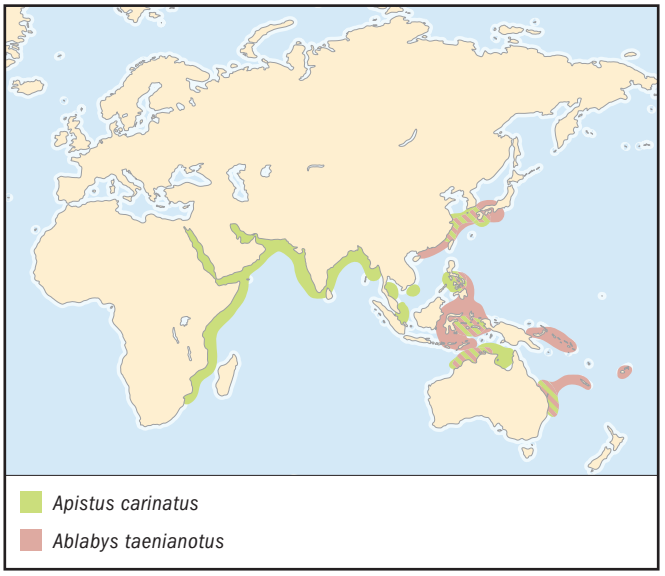
PHYSICAL CHARACTERISTICS
Reaches 6.7 in (17 cm) maximum length. An orange, bronze, or gray scorpionfish, with greatly expanded pectoral fins and free pectoral rays, similar to those seen in sea robins and stingfishes. Becomes increasingly white ventrally, with a characteristic ocellated black spot on the posterior half of the spinous dorsal fin.

DISTRIBUTION
Widely distributed species found throughout the Indian Ocean and the western Pacific. They range from South Africa north to the Red Sea and Persian Gulf in the western Indian Ocean and from China and Japan south to Australia in the Pacific.

HABITAT
Typically collected on the continental shelf on muddy or sandy bottoms at depths ranging from 66–197 ft (20–60 m).

BEHAVIOR
The ocellated waspfish, like sea robins and stingfishes, moves slowly over the seafloor, searching through the soft bottom with its free pectoral rays. It is highly venomous.

FEEDING ECOLOGY AND DIET
Like most scorpionfishes, the ocellated waspfish feeds primarily on crustaceans and fishes; it is preyed upon by humans.



REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of the ocellated waspfish.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The ocellated waspfish is a commercially important food fish that is collected by trawls and seines in small quantities. This fish is sold in markets either fresh or dried and salted. ◆

Crested scorpionfish
Ptarmus jubatus

FAMILY
Aploactinidae

TAXONOMY
Ptarmus jubatus Smith, 1935, Natal Coast, South Africa.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 3.9 in (10 cm) maximum length. As is implied by the common name of their family, velvetfishes such as the crested scorpionfish have a derived "knobby" scale morphological feature that makes them feel velvety to the touch. The single, continuous dorsal fin originates over the eye. This species typically varies in coloring from light brown to black. It can be covered with white spots and has a black stripe through its eye.

DISTRIBUTION
Can be found from southern Mozambique down to the Natal coast of South Africa.

HABITAT
Usually found in relatively shallow water, particularly in weedy areas.

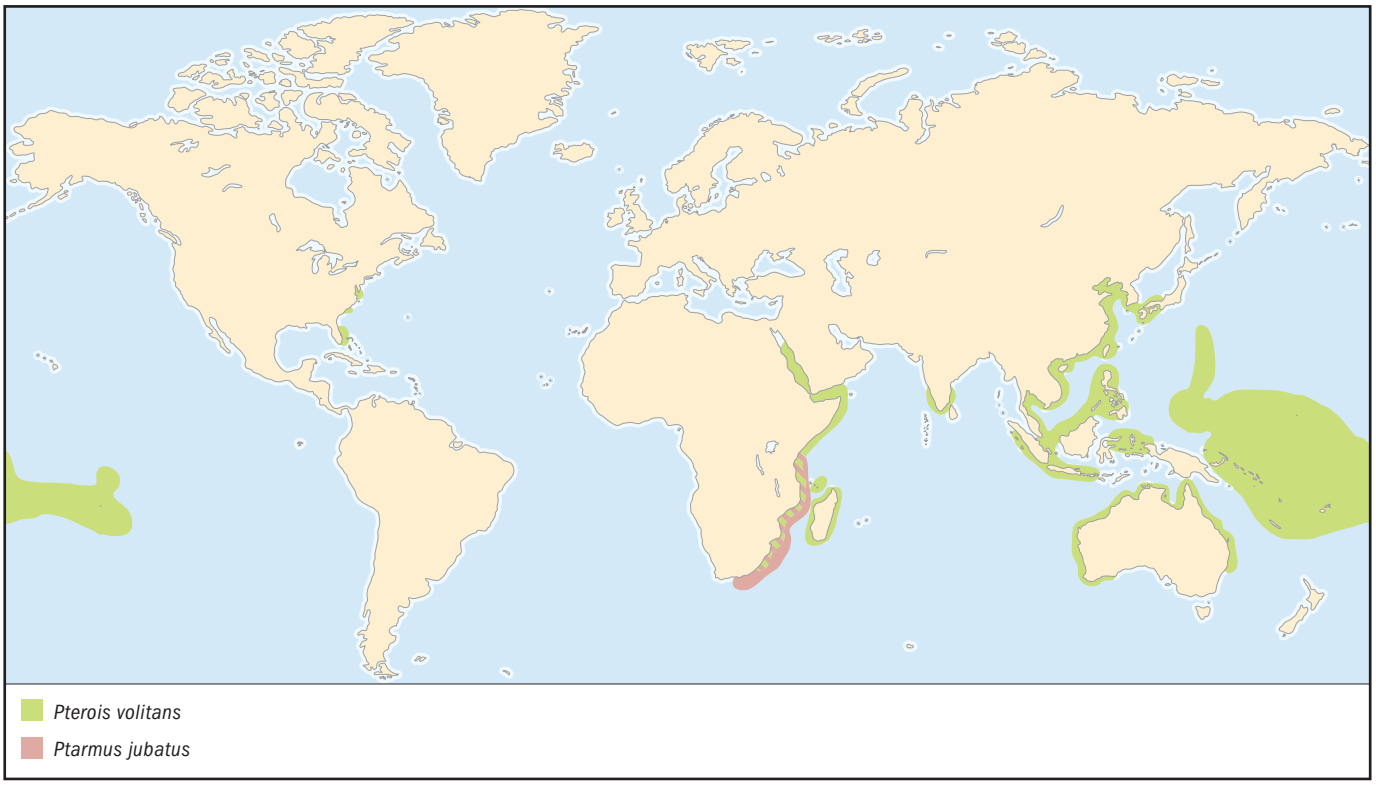
BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
The diet of these fishes is unknown, but it is likely that they feed primarily on crustaceans. May be eaten by larger fishes.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not collected commercially and reported to be nonvenomous. ◆



Spotted coral croucher
Caracanthus maculatus

FAMILY
Caracanthidae

TAXONOMY
Caracanthus maculatus Gray, 1831), Tuamotu Island, Polynesia.

OTHER COMMON NAMES
Japanese: Dango-okoze.

PHYSICAL CHARACTERISTICS
Reaches 1.6 in (4 cm) in maximum length. Small, rounded, laterally compressed fishes, with small pectoral fins and pelvic fins with one spine and three rays. Their bodies are covered with papillae, giving them a furry or velvet-like appearance. Typically gray laterally, with numerous red spots on the dorsal and lateral surfaces.

DISTRIBUTION
Can be found from southern Japan to southeastern Polynesia, Australia, and the East Indies.

HABITAT
These inconspicuous fishes can be found among the branches of *Acropora*, *Poecillopora*, and *Stylophora* corals.

BEHAVIOR
Coral crouchers spend most of their time among the branches of corals, rarely venturing away from the coral head. It is not known whether they are venomous.

FEEDING ECOLOGY AND DIET
Little is known about the feeding ecology and diet of these enigmatic scorpionfishes.

REPRODUCTIVE BIOLOGY
Little is known about the reproduction of the spotted coral croucher.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
These fishes are too small to be commercially fished, but they are occasionally collected for the aquarium trade, where they are marketed as "gumdrops." ◆

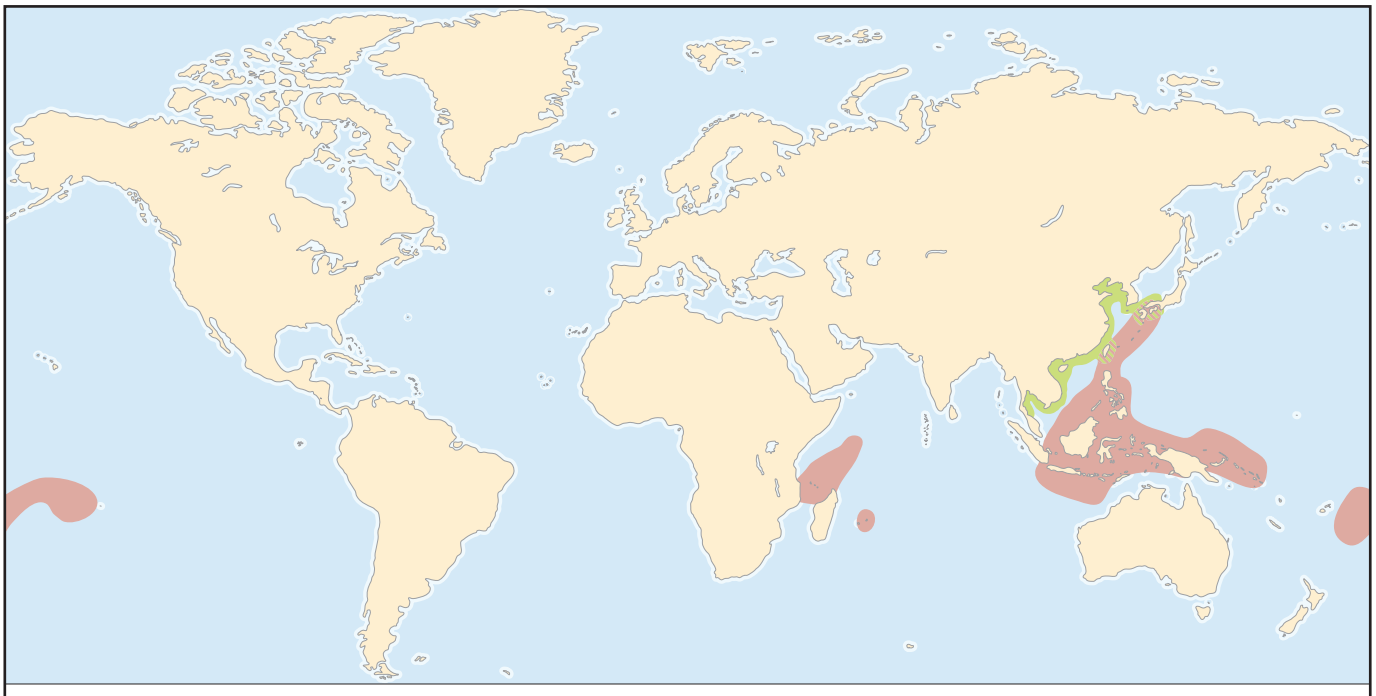
South American pigfish
Congiopodus peruvianus

FAMILY
Congiopodidae

TAXONOMY
Congiopodus peruvianus Cuvier, 1829, San Lorenzo Island, Peru.

OTHER COMMON NAMES
Spanish: Pez chancho, chanchito; Japanese: Apachhi.

PHYSICAL CHARACTERISTICS
Grows to 11 in (28 cm) maximum length. Laterally compressed, with a single, sail-like dorsal fin. Snout has a single nostril on each side. The body is light brown with irregular dark blotches and spots, particularly on the dorsal fin. Additionally, there is a black band on the caudal peduncle and caudal fin.



DISTRIBUTION
This pigfish can be collected off the coast of South America in both the southeastern Pacific and southwestern Atlantic.

HABITAT
This is a demersal species that usually is taken at depths from 66–492 ft (20–150 m).

BEHAVIOR
As is seen in some other scorpionfishes, the molting or shedding of skin has been reported in congiopodids. These scorpionfishes are not venomous.

FEEDING ECOLOGY AND DIET
Very little is known about the diet of pigfishes. May be eaten by larger predatory fishes.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Although the flesh of this species is edible, it is rarely eaten. ◆

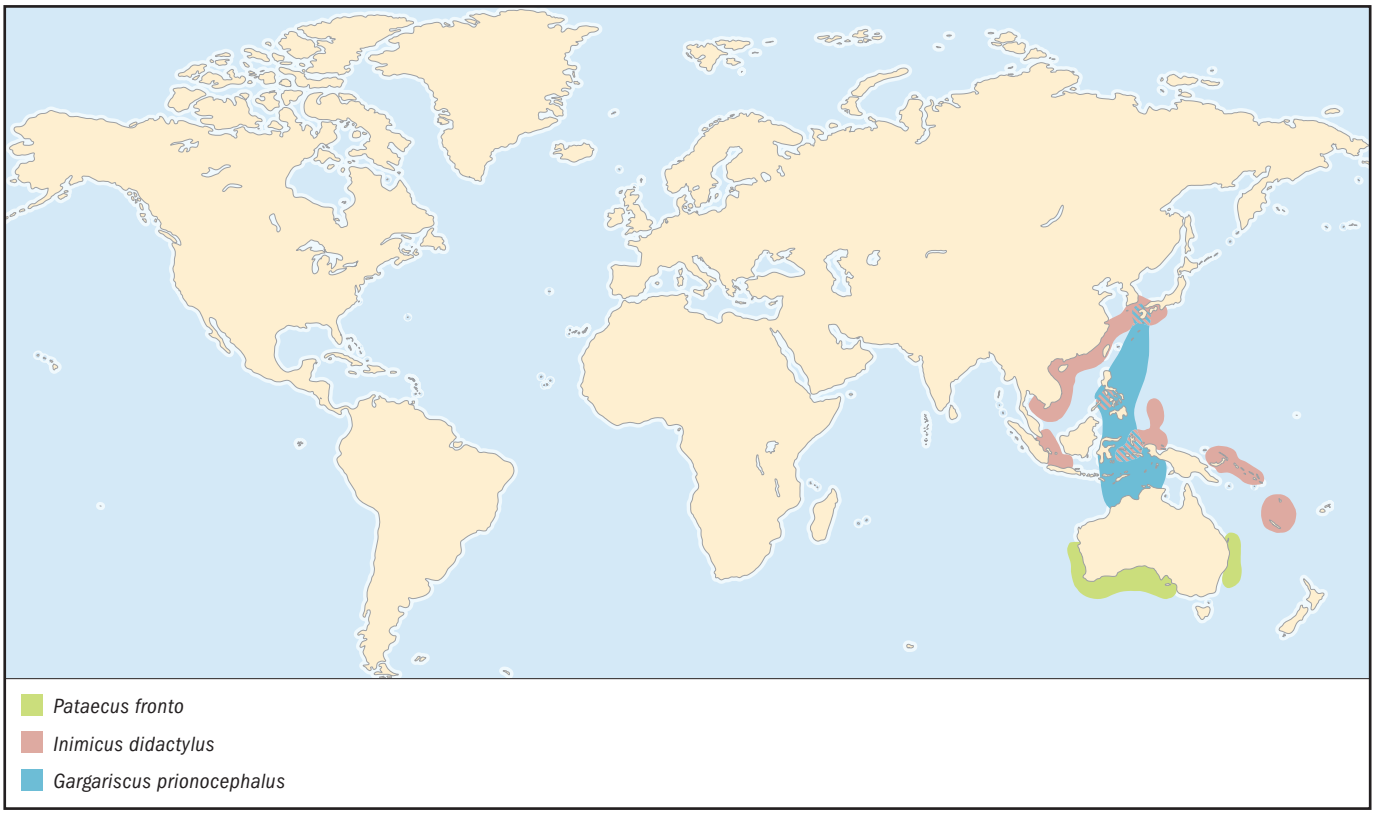
Red indianfish
Pataecus fronto

FAMILY
Pataecidae

TAXONOMY
Pataecus fronto Richardson, 1844, Southern Australia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 11.8 in (30 cm) maximum length. An unusual-looking fish that is highly compressed, with a high dorsal fin con-



fluent with the caudal fin. The color varies but usually ranges from brownish orange to bright red. Their bodies often are covered by dark blotches dorsally.

DISTRIBUTION
Found in southern Australia from southern Queensland to eastern Victoria.

HABITAT
It is difficult to observe red indianfishes because of their excellent camouflage. When they are seen, they are found in rocky reefs and estuaries, often in similarly colored sponge beds.

BEHAVIOR
Red indianfishes often shed the outer layer of skin to help get rid of epibiotic growth (algae or bryozoans), which acts as camouflage. Additionally, these fishes have an unusual "swimming" style that mimics a dead leaf floating in the water; they basically twist and spin as the fall back to the sea floor. The red indianfish is not venomous.

FEEDING ECOLOGY AND DIET
Little is known about the diet of red indianfishes, but their diet probably consists primarily of shrimps and other crustaceans. May be eatern by larger predatory fishes.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of these fishes.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is not commercially fished, but they are occasionally captured in commercial trawl nets. ◆

Belalang
Gargariscus prionocephalus

FAMILY
Peristediidae

TAXONOMY
Gargariscus prionocephalus Duméril, 1869, Sulawesi, Indonesia.

OTHER COMMON NAMES
Japanese: Onikihôbô.

PHYSICAL CHARACTERISTICS
Reaches 11 in (28 cm) maximum length. Coloring is orange to red, with black bands on the dorsal and pectoral margins. Its body is entirely encased in spine-bearing plates. There are seven large barbels on the lower jaw and a pair of sculptured rostral projections on the snout.

DISTRIBUTION
Distributed from Japan and the Philippines south to northern Australia.

HABITAT
A deepwater species that typically is taken on the continental shelf. It is collected at depths greater than 657 ft (200 m).

BEHAVIOR
Little is known. They do not appear to be venomous.

FEEDING ECOLOGY AND DIET
The diet consists primarily of crustaceans. Preyed upon by larger predatory fishes.

REPRODUCTIVE BIOLOGY
Nothing is known about their reproductive biology, but other armored gurnards produce small pelagic eggs.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This species is rare, so it is not of commercial importance. ◆

Red lionfish
Pterois volitans

FAMILY
Scorpaenidae

TAXONOMY
Pterois volitans Linnaeus, 1758, Moluccas Island, Indonesia.

OTHER COMMON NAMES
English: Volitan lionfish, butterfly cod, red firefish, turkeyfish; French: Poisson volant; German: Rotfeuerfisch; Japanese: Hana-minokasago, ominokasago.

PHYSICAL CHARACTERISTICS
Reaches 13.8 in (35 cm) maximum length. One of the most easily recognized of all marine fishes. The most striking features of the red lionfish are its banded (reddish to black) head and body and its unique pectoral configuration. The long, flowing pectoral rays have varying degrees of connecting membranes, giving them the distinctive appearance of separate threadlike projections. The dorsal and anal fins are covered with dark rows of spots on a clear to yellowish background. All of the non-pelvic spines—these include the pectoral, anal, and dorsal spines—are venomous.

DISTRIBUTION
A wide-ranging species found throughout the Indo-Pacific region. Recently, populations of the red lionfish have become established on the Atlantic coast of the United States, presumably released by aquarium wholesalers in Florida following Hurricane Andrew in 1992. This introduced species has been collected from the Florida Keys north to North Carolina and the southern coast of Long Island, New York.

HABITAT
Usually found in lagoon and seaward reefs. Typically, it is a fairly shallow-water species, but it can be found as deep as 164 ft (50 m). They tend to hide among rocks or in caves during the day.

BEHAVIOR
The audacity of the colors of this species is a clear warning sign for its exceedingly venomous spines. This species flexes its pectoral fins quickly to charge aggressors with its extended dorsal spines.

FEEDING ECOLOGY AND DIET
This species, like most species of *Pterois*, is a voracious predator that feeds primarily on small fishes, shrimps, and crabs. It has been reported that it can eat as much as 8.2 times its body weight per year. Feeds primarily at night, when it uses its widespread pectoral fins to trap prey into a corner. Preyed upon by humans.

REPRODUCTIVE BIOLOGY
Primarily solitary, but a single male forms aggregations with females for mating. Courtship begins at twilight and is initiated by the male. Females generally produce two tubes composed of mucus and between 2,000 and 15,000 eggs. Shortly after the females release the eggs, the tubes swell with seawater and are penetrated by the male's sperm. Fertilization proceeds, and the larvae hatch after 36–48 hours.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected in large numbers for the aquarium trade. Despite its venomous nature, the red lionfish also is harvested commercially for food. ◆

Merlet's scorpionfish
Rhinopias aphanes

FAMILY
Scorpaenidae

TAXONOMY
Rhinopias aphanes Eschmeyer, 1973, New Caledonia.

OTHER COMMON NAMES
English: Weedy scorpionfish.

PHYSICAL CHARACTERISTICS
Grows to 10.2 in (26 cm) maximum length. A compressed, large-headed scorpaenid, with an upturned mouth. Typically yellow and black, forming a paisley or "mazelike" appearance. Predominately brown, green, and black specimens also have been recorded. The body and head of this species are covered with cirri and other fleshy appendages.

DISTRIBUTION
Has been collected in northeastern Australia, New Caledonia, New Guinea, and southern Japan but probably is more widespread in the western Pacific.

HABITAT
Little is known about this cryptic species, but it often is found sitting on corals and appears to be most common on coral slopes.

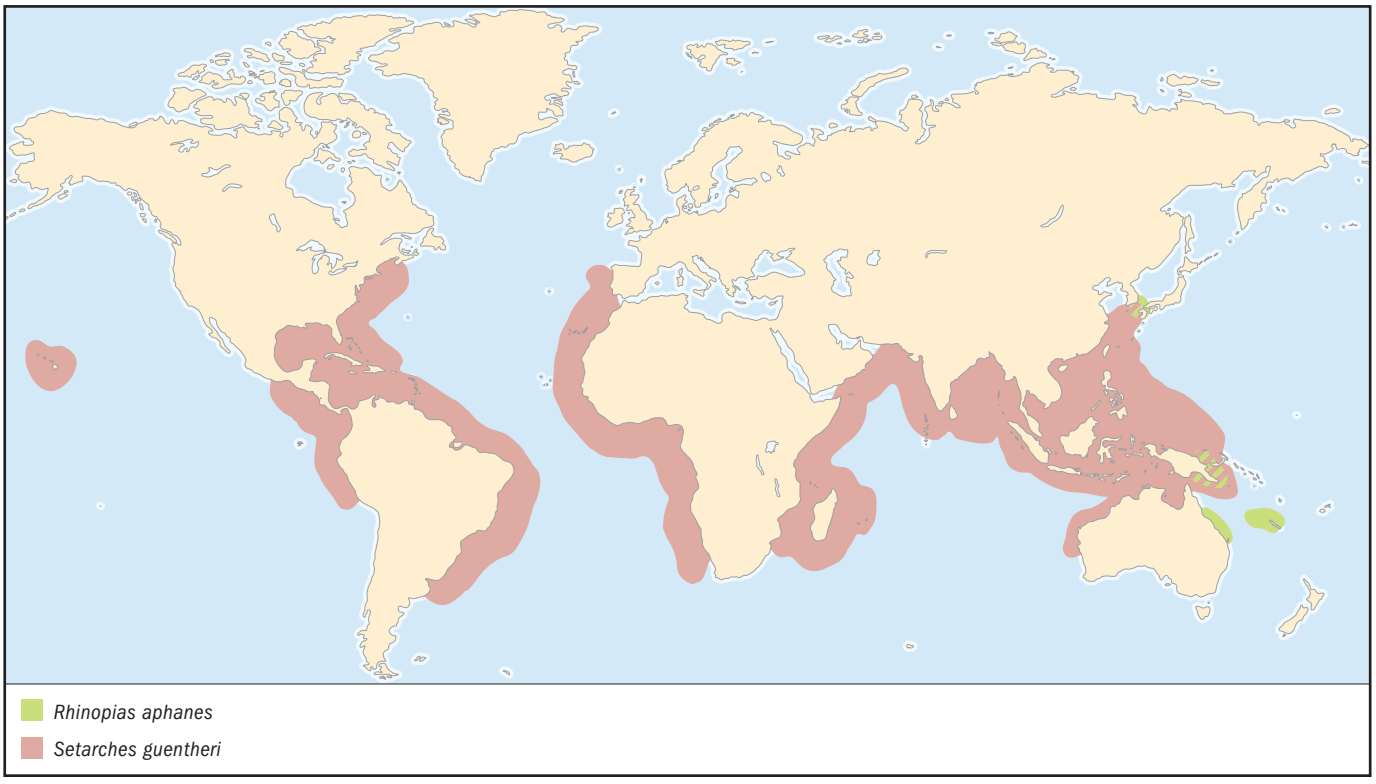
BEHAVIOR
Like many other scorpaenoid fishes, this cryptic fish appears to shed its skin periodically to prevent the buildup of too much epibiotic growth. The presence or absence of venom in this species has not been reported.

FEEDING ECOLOGY AND DIET
The diet is unknown, but most other species of *Rhinopias* feed primarily on crustaceans and small fishes.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not commercially fished, but numerous other *Rhinopias* species are prized aquarium specimens. It is likely that Merlet's scorpionfish may already be imported for the aquarium trade. ◆



California scorpionfish
Scorpaena guttata

FAMILY
Scorpaenidae

TAXONOMY
Scorpaena guttata Girard, 1854, Monterey, California.

OTHER COMMON NAMES
English: Sculpin; French: Rascasse californienne; Spanish: Rascacio californiano, escorpión californiano.

PHYSICAL CHARACTERISTICS
Reaches 16.5 in (42 cm) maximum length. Like most scorpaenids, it is a well-camouflaged, spiny, massive fish. The coloring varies widely, from a deep red through light brown. Black, dark brown, and maroon spots cover the body and fins.

DISTRIBUTION
Found from Santa Cruz, California, south to southern Baja California. This species also is found in the Gulf of California.

HABITAT
These scorpionfishes are most abundant on hard bottoms, particularly rocky reefs, caves, and man-made structures, such as wrecked ships. Additionally, they can be found on muddy and sandy bottoms.

BEHAVIOR
Although most scorpionfishes and their allies are venomous, the California scorpionfish is the most venomous fish regularly collected off the California coast.

FEEDING ECOLOGY AND DIET
The diet of these predators primarily consists of crabs, but small fishes, octopi, and other crustaceans also are eaten.

REPRODUCTIVE BIOLOGY
Unlike most marine fishes, females produce eggs that are imbedded within the gelatinous walls of pear-shaped structures that float near the surface. After five days, the eggs hatch within these structures. The larval fishes that emerge have an integument that has an inflated appearance and is vesiculate. The larvae remain in plankton until they reach the length of 0.6–0.8 in (15–20 mm), upon which they settle in their adult habitat.

CONSERVATION STATUS
Although the species represents a fairly important fishery, they currently are not threatened as are some of their rockfish relatives.

SIGNIFICANCE TO HUMANS
Supports an important commercial and sport fishery in southern California and Ensenada, Baja California. Most fishes are taken in the spring and summer months, when commercial fishermen target spawning aggregations using hook and line, gill nets, and otter trawls. ◆

Bocaccio
Sebastes paucispinis

FAMILY
Sebastidae

TAXONOMY
Sebastes paucispinis Ayres, 1854, California.

OTHER COMMON NAMES
English: Rock salmon; Spanish: Rocote bocaccio.

PHYSICAL CHARACTERISTICS
Grows to 37.4 in (95 cm) maximum length. Bocaccios are one of the most elongate rockfishes in California and one of the least spiny rockfishes. They tend to be reddish brown on the dorsal surface, pink or brown on the flanks, and silver ventrally. Juveniles and small adults are reddish brown with dark spots.

DISTRIBUTION
Widespread from Alaska to Baja California. They are most abundant from British Columbia to Washington.

HABITAT
Juveniles typically are collected in shallow waters under drifting kelp mats that have broken free. Adults form benthic aggregations over hard and rocky bottoms at depths ranging from 164 to 984 ft (50–300 m).

BEHAVIOR
Bocaccios are a mobile rockfish. Tagged juveniles often are recaptured 60–80 mi (97–129 km) away from their point of origin. As with many other scorpaenoids, the bocaccio is venomous, but the venom is comparatively weak (although local fishermen suggest that they are the most venomous of the rockfishes).

FEEDING ECOLOGY AND DIET
Juveniles feed on small fishes, particularly other rockfishes. Adults feed on rockfishes, sablefishes (Anoplopomatidae), anchovies (Engraulidae), and squids. Eaten by larger fishes and pinnipeds.

REPRODUCTIVE BIOLOGY
As with all sebastids, the bocaccio is viviparous (live bearing). Large females can produce more than two million eggs per season, which are released as larvae in two or more batches. Rockfish larvae remain in the upper 263 ft (80 m) of the water column for several months. This stage is followed by a pelagic juvenile stage that lasts one to several months, after which the larvae settle.

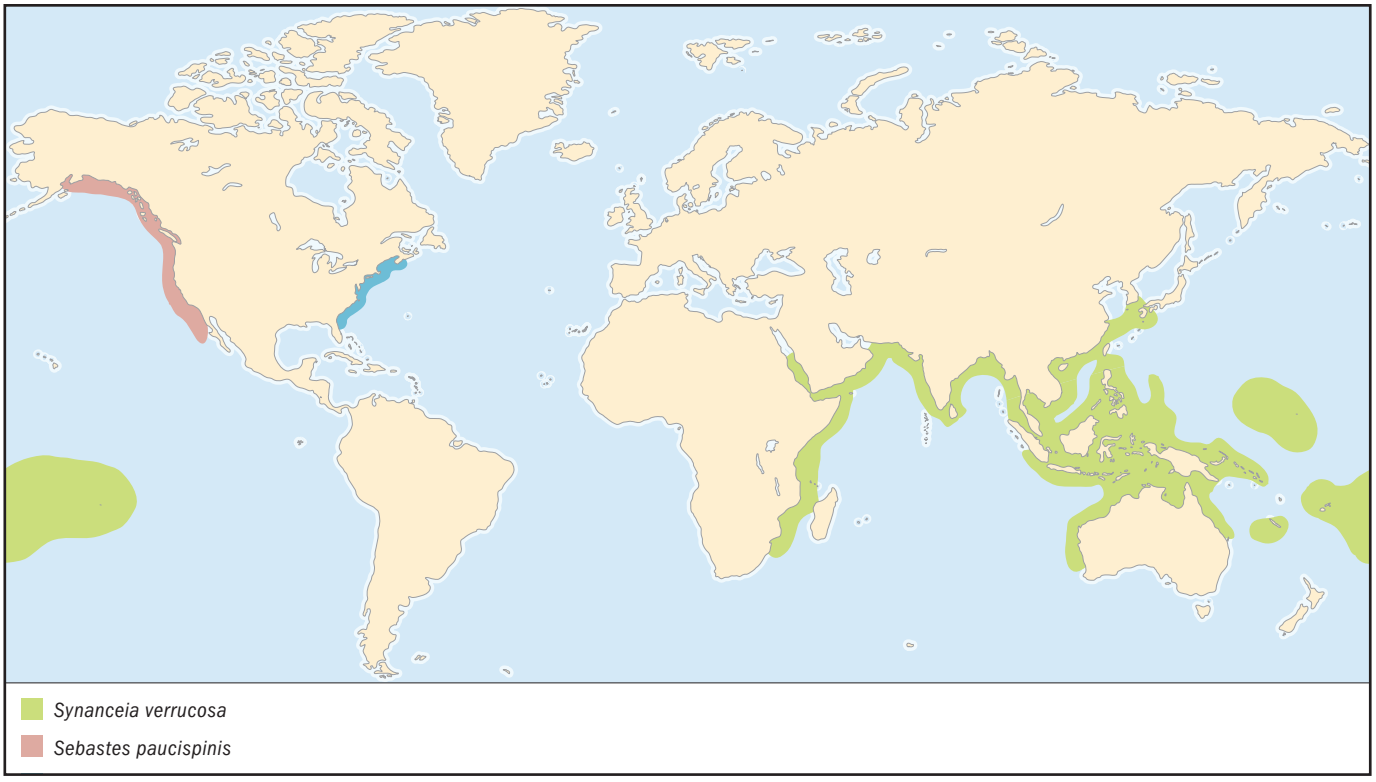
CONSERVATION STATUS
The bocaccio is the only Critically Endangered scorpaenoid. This listing suggests that the population size has decreased by more than 80% in about the last ten years of the twentieth century, owing to the pressure of overfishing and the low minimum population doubling time, which is longer than 14 years.

SIGNIFICANCE TO HUMANS
As their population decline suggests, bocaccios traditionally have been a very important commercial and recreational food fish in the eastern Pacific. When they were more abundant, they represented more than 14% of the total marine recreational catch of California. ◆

Deepwater scorpionfish
Setarches guentheri

FAMILY
Setarchidae

TAXONOMY
Setarches guentheri Johnson, 1862, Madeira.



OTHER COMMON NAMES
English: Channeled rockfish; French: Rascasse serran; Spanish: Rascacio serrano; Japanese: Shirokasago.

PHYSICAL CHARACTERISTICS
Grows to 9.4 in (24 cm) maximum length. Typically gray or a shade of orange or pink. As is seen with many deepwater fishes, the skeleton is poorly ossified, and the head is cavernous.

DISTRIBUTION
Described as the most widely distributed scorpaenoid, because it has been collected worldwide in all tropical and temperate deep waters.

HABITAT
A benthic species that lives on or near the bottom at depths between 591–2,297 ft (180–700 m).

BEHAVIOR
Nothing is known about the behavior of this species.

FEEDING ECOLOGY AND DIET
Preliminary investigations into the diet of this species suggest that it eats deepwater crustaceans, including oplophorids and amphipods.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
No commercial fishery exists for this deepwater species, although it can be found occasionally in eastern Atlantic fish markets. ◆

Bearded ghoul
Inimicus didactylus

FAMILY
Synanceiidae

TAXONOMY
Inimicus didactylus Pallas, 1769, Indian Ocean.

OTHER COMMON NAMES
English: Demon stinger, popeyed sea goblin, spiny devilfish; Japanese: Hime-oniokoze.

PHYSICAL CHARACTERISTICS
Grows to 7.9 in (20 cm) maximum length. The bearded ghoul is best recognized by the shape of its head and its elongate pectoral fins, which it uses for crawling along the bottom. This species can be distinguished by the pattern on the medial surface of its pectoral fin, which has a broad, dark, transverse bar that may be streaked.

DISTRIBUTION
Distributed from southern Japan and Indonesia to Australia, the Solomon Islands, and New Caledonia.

HABITAT
A benthic species found on open sandy or silty bottoms, particularly in estuaries, lagoons, and seaward reefs.

BEHAVIOR
A particularly venomous species that is capable of killing a human. Like most stonefishes, this species is a lie-and-wait predator that relies on its cryptic coloration and body form to surprise prey.

FEEDING ECOLOGY AND DIET
Feeds primarily on crustaceans, but small fishes also are preyed upon.

REPRODUCTIVE BIOLOGY
Little is known about the reproductive biology of this species.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Because of its small size, this species is not fished commercially; however, despite the fact that these fishes are highly venomous, they are collected occasionally for the aquarium trade, where they are sold as "popeyed sea goblins." ◆

Reef stonefish
Synanceia verrucosa

FAMILY
Synanceiidae

TAXONOMY
Synanceia verrucosa Bloch and Schneider, 1801, Indian Ocean.

OTHER COMMON NAMES
English: Stonefish, dornorn; French: Poisson pierre commun; Japanese: Oni-darumaokoze.

PHYSICAL CHARACTERISTICS
Reaches 15.7 in (40 cm) maximum length. The reef stonefish is among the best-camouflaged species in the world. Most of these fishes look like encrusted rocks or pieces of coral. Most specimens are dark brown or gray, but they usually have patches of yellow, red, or orange.

DISTRIBUTION
This is the most widely distributed stonefish. It can be found throughout the Indo-Pacific from Africa to the Tuomoto Archipelago.

HABITAT
Usually found living among rubble, on coral bottoms, or under rocks or ledges. They also are found on sandy or muddy bottoms, where they often bury themselves.

BEHAVIOR
This is the world's most venomous fish. Unlike most scorpaenoids, the stonefishes have grooves in their dorsal spines that act like syringes to deliver venom.

FEEDING ECOLOGY AND DIET
This species feeds primarily on small fishes and crustaceans that swim by.

REPRODUCTIVE BIOLOGY
Stonefishes are typically solitary creatures, but they do form larger aggregations for mating. The reef stonefish has external fertilization, and produces comparatively large eggs.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Despite the extreme danger associated with collecting this species, there are commercial fisheries for both dead and live fish markets. In addition to their commercial fishery, stonefishes make their way into the aquarium trade. The sting of the stone fish is extremely painful and is followed by rapid swelling around the wound. The severity of the response is related to the depth of the penetration by the spines. The treatment of the wound consists of bathing the stung area in very hot water until the victim can be hospitalized. For more serious stings, it is often advisable for stonefish antivenin to be given intramuscularly. The stonefish antivenin is composed of purified antibodies against stonefish venoms and venom components. These antibodies are harvested from laboratory animals, which are given small doses of the venom. Eventually, these animals build up a tolerance to the venom, which allows them to produce the large quantity of venom antibodies required for the antivenin. ◆

Cockatoo waspfish
Ablabys taenianotus

FAMILY
Tetrarogidae

TAXONOMY
Ablabys taenianotus Cuvier, 1829, Mauritius.

OTHER COMMON NAMES
English: Rogue fish.

PHYSICAL CHARACTERISTICS
Grows to 5.9 in (15 cm) maximum length. A strongly compressed waspfish with a sail-like dorsal fin that originates above the eye. Cockatoo waspfishes are reddish brown with black lines and black and white blotches sprinkled over the dorsal and lateral surfaces.

DISTRIBUTION
Widely distributed in the western Pacific as far north as Japan and south to Australia and Fiji. Can be found as far west as India and as far east as the Society Islands.

HABITAT
A cryptic species that typically is collected among seaweed in littoral or rocky intertidal habitats in shallow depths to 263 ft (80 m).

BEHAVIOR
Cockatoo waspfishes tend to be more active at dusk or night. As is seen in some other scorpaenoids, this species often is found rocking back and forth in response to the surge, to mimic the seaweed that surrounds it. This species is quite venomous.

FEEDING ECOLOGY AND DIET
Like many waspfishes, this species feeds primarily on small crustaceans, particularly shrimps, and smaller fishes.

REPRODUCTIVE BIOLOGY
Little is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not commercially fished but collected for the aquarium trade. ◆

Red gurnard
Chelidonichthys spinosus

FAMILY
Triglidae

TAXONOMY
Chelidonichthys spinosus McClelland, 1844, China.

OTHER COMMON NAMES
Japanese: Hôbô.

PHYSICAL CHARACTERISTICS
Reaches 15.7 in (40 cm) maximum length. Head encased in bony armor with short rostral projections. Body coloration varies from brown to light orange or red when under stress. The dorsal surface of this species has brown patches, and the inner surface of the pectoral fins is olive to dark green, with scattered blue or white spots.

DISTRIBUTION
Found from southern Hokkaido (Japan) south to the South China Sea.

HABITAT
Found on sandy bottoms.

BEHAVIOR
The red gurnard, like all sea robins, spends much of its time "walking" on the seafloor, using its free pectoral rays to probe the sediment for food. Capable of making sounds using drumming muscles that are beaten against the gas bladder. Venom has not been found.

FEEDING ECOLOGY AND DIET
The diet consists mainly of various crustaceans and mollusks. Preyed upon by larger predatory fishes.

REPRODUCTIVE BIOLOGY
The red gurnard produces large pelagic eggs. There have been numerous reports of increased male grunting during the breeding season, suggesting that auditory signals are important in mate selection.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An excellent food fish. Taken by trawlers throughout its range. ◆

Striped sea robin
Prionotus evolans

FAMILY
Triglidae

TAXONOMY
Prionotus evolans Linnaeus, 1766, North or South Carolina, United States.

OTHER COMMON NAMES
French: Grondin volant; Spanish: Rubio volador.

PHYSICAL CHARACTERISTICS
Reaches 17.7 in (45 cm) maximum length. Characterized by a large bony head with many ridges and spines and a bifurcate lateral line on the tail. The striped sea robin is white ventrally, with various shades of golden, brown, and orange on the sides and dorsal surface. It often has dark saddles underneath the dorsal fins and is best distinguished from other species by the two thin, black stripes running along the side of the body. The dorsal stripe runs the entire length of the fish along the lateral line, and the smaller, incomplete stripe is situated below. The tail has two black bars with a light area between them.

DISTRIBUTION
Found from southern Nova Scotia down the Atlantic Coast of North America to northeastern Florida. Typically collected at depths of less than 200 ft (61 m) but have been found at depths as great as 550 ft (168 m).

HABITAT
Usually found on sandy bottoms. It often can be taken in inshore estuaries or over reefs, particularly in summer months.

BEHAVIOR
The striped sea robin uses its free pectoral rays to "walk" along the seafloor in search of prey. The sea robins along the Atlantic Coast of North America are famous for their ability to produce sounds by "beating" the swim bladder muscles against the gas-filled swim bladder, making a characteristic grunting noise. Typically, the striped sea robin is found offshore, but the species makes migrations into the deeper, more saline estuaries for breeding. This species is not venomous.

FEEDING ECOLOGY AND DIET
The diet consists mainly of crustaceans, mollusks, and fishes. Preyed upon by larger predatory fishes.

REPRODUCTIVE BIOLOGY
Produces pelagic eggs. This species appears to breed in deeper estuarine environments, typically in the summer months from May to October. It seems clear that sound plays a role in choice of mate.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The striped sea robin is a commercially important fish. It is collected and used for human consumption, fishmeal, bait, pet food, and fertilizer. Smaller specimens often are collected for the aquarium trade, though they grow too large for most home aquaria. ◆

Resources

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William Leo Smith, MS

Scorpaeniformes III

(Greenlings, sculpins, and relatives)

Class Actinopterygii
Order Scorpaeniformes
Number of families 10

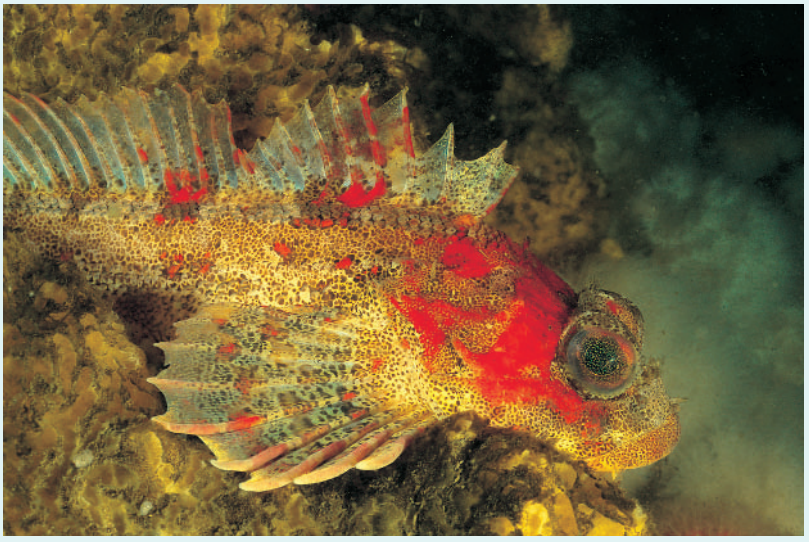


Photo: The red Irish lord (*Hemilepidotus hemilepidotus*) is one of the most beautiful sculpins. It can be found in a number of different colors. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The Scorpaeniformes, the mail-cheeked fishes, are united by the presence of a bony ridge called a "suborbital stay" on the cheek, running horizontally below the eye and providing an armored look to the head of most species. The suborbital stay is a posterior extension of the second infraorbital (eye socket) bone. In the sculpins (Cottoidei), this suborbital stay tends to be very prominent, while in the greenlings (Hexagrammoidei) it is not easily seen.

The ancestral scorpaeniform stock is considered to have derived from a generalized percoid (perch) fish. That is to say, cottoid (sculpin) and hexagrammoid (greenling) fishes are among the most recently evolved, advanced fishes. The Scorpaeniformes is the fourth largest order of fishes, including about 29 families, about 260 genera, and 1,400 species. Most of these fishes are bottom-dwelling or live near the seabed. Nine families are covered in this chapter, with the remainder covered in Scorpaeniformes I and II.

Among the scorpaeniform fishes, the suborder Cottoidei includes between seven and 13 families in modern classifications. Historically, various additional cottoid families have been distinguished, often containing only one species. The most prominent families include the sculpins (Cottidae, with 305 species in 70 genera), fathead sculpins (Psychrolutidae, with 11 species, five genera), poachers (Agonidae, with 49 species, 20 genera), lumpfishes (Cyclopteridae, with 27 species, eight genera), and snailfishes (Liparididae, with 195 species, 13 genera). Also within the Cottoidei are two families of Lake Baikal fishes, the Cottocomephoridae (Baikal sculpins, with 24 species, eight genera), and Comephoridae (Baikal oilfishes, with two species, one genus). The Baikal oilfishes are distinguished by being the only viviparous (live-bearing) cottoid fishes. A monotypic (one species) family, the Normanichthyidae, consists of one marine species off Chile that is often included within the Cottoidei. That species, *Normanichthys crockery*, would be the only cottoid fish having a swim bladder, but the anatomical description by Yabe and Uyeno (1996) concludes that the family is of uncertain systematic position within the Scorpaeniformes, and not correctly within the Cottoidei. Other families common in various classifications include the Cottunculidae (here included within the Psychrolutidae), the Icelidae (sometimes distinguished from Ereuniidae, both within the Cottidae here), and the Hemitripteridae (here included within the Cottidae). The species in the Psychrolutidae are usually included within the Cottidae in older works, but Jackson and Nelson (1998) have described the unique features of sensory canals and associated bones on the head which, together with other characters, distinguish the fathead sculpins from the other sculpin species. Some classifications place the liparidid fishes within the Cyclopteridae. Cottoid fishes probably first appeared in the North Pacific and only invaded the Arctic and North Atlantic Oceans 3.5 million years ago.

The zoogeography of cottoid fishes centers on the Pacific coast of North America. The other scorpaeniform suborder considered within this chapter is the Hexagrammoidei, the greenlings, which includes the largest family of fishes endemic to the North Pacific, the Hexagrammidae (11 species, five genera). Some classifications separate the combfishes into a separate family, the Zaniolepidae. Another family usually included within the Hexagrammoidei is the Anoplopomatidae, which includes the sablefish (*Anoplopoma fimbria*) and the skilfish (*Erilepis zonifer*). Sometimes the skilfish is separated into the monotypic family Erilepidae, also with these two families separated from other hexagrammoids into the Anoplopomatoidei.

A tidepool sculpin (*Oligocottus maculosus*) in the Pacific Ocean, near the United States. Each sculpin changes color to match its tidepool, or buries itself in sand. If it is washed out of its tidepool, it uses its sense of smell and returns to its own pool. (Photo by Nancy Sefton/Photo Researchers, Inc. Reproduced by permission.)

Physical characteristics

The hexagrammoid fishes are perhaps the most generalized scorpaeniform fishes, resembling many perciform fishes. Hexagrammoid fishes have no head spines, and they include some of the only pelagic species, fish which have a fusiform body shape adapted to swimming in open water. Fishes of the genus *Hexagrammos* have multiple lateral lines, although Wonsettler and Webb (1997) have demonstrated that only the central trunk canal is innervated, as in other teleost fishes, so the biological significance of the other four, non-functional lateral lines, has become a mystery. As with the more diverse cottoids, most hexagrammids are adapted to dwelling on the sea bottom. They have no swim bladder and the pectoral fins are enlarged, with the lower edge attached further forward than the top edge, so that the fish can rest on these fins like a pair of elbows.

In the Cottoidei, extreme divergence of structure and function have yielded some of the most unusual-looking of all fishes. All cottoids lack the swim bladder and most have a flattened head, as well as enlarged pectoral fins like the greenlings. There are many skin adaptations, including loss of scales or modification of scales into bony plates. The Psychrolutidae (fathead sculpins) have flaccid bodies (puffy skin) with reduced skeletal structure. The Agonidae (poachers) have armor plates over their body, have all fin rays unbranched, and have lost the suborbital stay. The Cyclopteridae (lumpfishes or lumpsuckers) have a globular body covered with tubercles and with the pelvic fins modified into a sucking disc. The Liparididae (snailfishes) also have a pelvic sucking disc, but the body is without scales and is elongate. The Cottidae (sculpins) include the greatest divergence in body form and size, which is perhaps why various families historically have been separated from this taxonomic grouping. All cottid fishes have a single pelvic fin spine (except one species lacking pelvic fins) and no anal fin spine; they usually have naked skin, sometimes with cirri, sometimes with scales, and sometimes with prickles. Cottids lack swim bladders and tend to have large, flattened heads, often with pronounced spines and often with large eyes.

Color and fin shape lend toward a camouflaged appearance in most of these fishes. Cottoid and hexagrammoid fishes often display sexual dimorphism in color, body size, fin shape, or other features. Many cottid species have prominent male copulatory organs.

Distribution

The Cottoidei and Hexagrammoidei center their distribution in the eastern North Pacific Ocean, but antitropical (both hemispheres) distributions occur for cottoids in some instances. The Psychrolutidae include North Pacific and North Atlantic species, plus several species off New Zealand, Australia, and South Africa. Cottids similarly occur in the Northern Hemisphere (but in both marine and fresh waters) and off New Zealand, eastern Australia, and Argentina. Liparidids occur in both warm and cold marine waters of all the world's oceans, although rarely in the Indian Ocean. The Cyclopteridae occur only in cold, marine waters of the Northern Hemisphere. Agonids are found in the North Pacific, North Atlantic, and off southern South America.

The unique families of Lake Baikal cottoid fishes have been mentioned. Molecular genetic studies of Baikal cottoids (Kirilchik and Slobodyanyuk, 1997) reveal close relatedness with freshwater cottids such as *Cottus bairdii* from Lake Michigan and *Cottus cognatus* from Lake Michigan and Siberia. The genus *Cottus* is very widely distributed across North America and Eurasia, and the different species are all a very generalized cottid body type. The Baikal cottoids, although closely related to other freshwater cottids, have radiated into 22 endemic Baikal species (another four cottocomephorid species also occurring in other drainages of Siberia).

Habitat

The microdistribution of any species relates to habitat preference. The Northeast Pacific distribution of most cottoid species is reflected in an analysis of fish community structure of rocky shorelines of the North Pacific, which is dominated by cottids. The rocky intertidal of the Pacific coast of North America is dominated by various species of *Artedius*, *Clinocottus*, and *Oligocottus*. Other cottid genera have very narrow depth preferences in shallow subtidal marine waters. For example, the longfin sculpin, *Jordania zonope*, was considered extremely rare prior to the advent of scuba diving, because it inhabits vertical rock surfaces that are not amenable to sampling with nets. Similarly, the manacled sculpin, *Synchirus gilli*, was considered very rare until divers discovered it on the feather boa kelp, *Egregia menziesi*, on outer Pacific coast shores. The feather boa kelp does not occur, however, in protected inland seas like the Strait of Georgia (British Columbia), where the manacled sculpin spawns in the holdfasts of another kelp species, *Alaria marginata*. For the majority of cottoid species, very little is known of precise habits and habitat preferences.

The diverse snailfishes (Liparididae) occur broadly in the world ocean over a very wide depth range from the intertidal zone to greater than 23,000 ft (7,010 m) depth. Again, very little precise habitat information is available for the vast ma-

jority of species. Since most snailfishes possess a pelvic sucking disc, however, it is presumed that smooth surfaces of plants, animals, or rocks provide substrate for many of these species. As with other cottoid fishes, different species may prefer shores exposed to waves and tidal currents versus protected shores.

The Lake Baikal sculpins have been investigated since the eighteenth century. The diversification of these species seems in great part related to different depth preferences. Lake Baikal, at 5,315 ft (1,620 m) depth, is the deepest lake in the world.

The reason why the less diverse freshwater cottoid fishes have been studied more intensely than the vast diversity of marine species is that freshwater habitats are more accessible. Perhaps the most accessible marine habitat is the tidepool, and intertidal cottoids have received disproportionate study, except in comparison with fish species of commercial importance. A problem with the study and interpretation of tidepool fishes, however, has to do with the human perspective. Since people can most readily work around tidepools during low tides and calm weather, our interpretation of tidepools tends to focus on ecological advantages of the tidepool during a low tide (in calm weather) rather than during high tides and storms. Thus, tidepools are considered to offer refuge from subtidal predators during low tides, rather than to offer refuge from turbulence during high tides. Habitat can have widely divergent values and characteristics under different conditions, so the interpretation of habitat preferences needs to be tempered by perspective.

Discussions of fish habitat implicitly consider only adults in most studies. Tidepool studies reveal, however, that early juvenile stages of cottid species can have different habitat requirements than adults. Larval stages occupy the planktonic realm, a completely different habitat than that of most adult cottoids. Larvae of rocky intertidal cottids of various species have been shown to avoid drifting with currents away from the shoreline or along the shoreline, so behavior during early life stages may be directed toward providing access to required habitat in later stages. The precise substrate preference of a cottoid larva at settlement from the plankton may not be the same substrate preference as an adult, but it will be a substrate that is a component of the adult habitat. Thus, growth stages shift only their relative position on the seabed within a general habitat.

Niche partitioning between species in terms of habitat preference (as with food preference) is examined for mechanisms that allow ecological separation that could have led to speciation. Again, interpretation often focuses only on adults. In addition, intertidal studies of cottids have led to different interpretations of competition than subtidal studies. The flathead sculpin, *Artedius lateralis*, and the padded sculpin, *Artedius fenestralis*, occupy very similar habitats in the rocky intertidal, yet their larvae occupy different depth ranges along the shoreline. The flathead sculpin settles from the plankton in surface waters, directly onto substrates in the intertidal, whereas larvae of the padded sculpin occupy slightly deeper water, so that they settle subtidally. Thus, habitat preferences in terms of depth provide ecological segregation of these two cottid species during the larval and early juvenile stages. Adults of these species do not necessarily have to display any behavioral differentiation in order for their speciation to be explained.

Behavior

As mentioned, developmental stages of a species may be expected to shift behavior, even though most investigation concerns only the adult stage. Since cottoid and hexagrammoid fishes lack a swim bladder, the planktonic larval and pelagic juvenile stage (if occurring) need to display behavioral solutions to negative buoyancy. In some species those behaviors reflect morphological specializations for the particular life stage, but other species may simply have to swim very energetically, which will affect food requirements and feeding behavior. Schooling only occurs in adults of some of the few pelagic species in these taxa, but larval stages appear capable of schooling in many of the species observed in aquarium settings.

The cryptic appearance of most cottoids, together with bottom dwelling habits, leads to predation threats that require adaptive behaviors. Chance observations have led to the discovery that the tadpole sculpin, *Psychrolutes paradoxus*, apparently has an emetic flavor that causes predators to cough them out upon ingestion. This species relies first on its cryptic appearance to prevent predation, then secondarily upon its noxious taste to cause rejection by predators.

Even though cottoids lack a swim bladder, they have big extrinsic swim bladder muscles. The buffalo sculpin, *Enophrys bison*, vibrates when grasped. Another defense behavior in this and other species is the flaring of the gill cover (with the bony suborbital stay) to expose spines that could deter ingestion.

Homing behavior is well documented in cottids that inhabit tidepools. Tagging studies have not been directed as much at subtidal species, but the demonstration of topographic familiarity in tidepool species may extend to other species inhabiting subtidal reefs with significant landmarks.

A painted greenling (*Oxylebias pictus*) in southern California. During mating season, the males often turn so dark in color that they appear black. (Photo by Gregory Ochocki/Photo Researchers, Inc. Reproduced by permission.)

A male lumpfish (*Cyclopterus lumpus*) guarding its eggs in the Gulf of Maine. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

The existence of homing behavior proves that learned familiarity with surrounding habitat is of significant survival value and that these fish are capable of exploiting that sort of advantage. Seasonal migrations encompass developmental shifts in habitat preference of young stages as well as reproductive behavior of adults.

Feeding ecology and diet

Because the many cryptic species of cottoid and hexagrammoid fishes tend to hide on the bottom of the sea, their feeding habits reflect the closeness of their prey species, which frequently include crustaceans such as amphipods, crabs, or shrimp. The functional morphology of the diverse mouth types in these taxa have been investigated in detail. Most studies of community feeding ecology in these fishes have been conducted with tidepool species.

In terms of mouth types, these fishes tend to feed either by pouncing on and engulfing their prey (ramming) or by drawing the prey into their mouth together with a stream of water by means of very rapid expansion of the gill covers (sucking). The third major type of prey capture in fishes (biting off a piece of a prey) is less well documented in cottoid and hexagrammoid fishes as a strict mode of feeding, although worms as prey may require biting behavior. Species that feed by suction tend to have small mouth openings, whereas species that engulf their prey have large, broad mouths. Different species can combine aspects of these different types of feeding behavior, and relative effectiveness of capture methods influences dietary preferences.

Beyond ingestion of prey, manipulation may be required to enable digestion. In *Asemichthys taylori* the vomerine teeth of the upper jaw are modified to enable punching holes in the shells of snail or clam prey so that soft tissues can be digested.

Two cottid species have been documented as switching to a substantially herbivorous diet as adults. These two species, *Enophrys bison* (buffalo sculpin) and *Clinocottus globiceps* (mosshead sculpin), have only been documented in terms of their gut contents. Gut morphology and digestive mechanisms such as gut acidity have not been studied in detail for these species. Ingestion of some seaweed may accompany predation on crustaceans inhabiting those seaweeds, but gut contents in these two sculpins, as in other taxa, can show the seaweed itself to be the preferred item. In the mosshead sculpin, the biting behavior that enables it to consume algae also enables it to remove pieces of tentacles from intertidal sea anemones (which have algae cells in their tissues).

The large eyes of most cottoid and hexagrammoid fishes would aid in detection of prey in very dim light. The sense of distant touch (lateral line and head canal system), however, enable detection of movement by potential prey in the vicinity of the fish. Psychrolutid fishes have particularly well-developed head canals with large pores. In the Agonidae, various species have the lower rays of their pectoral fins elongated beyond the webbing of the fin, so that they can rake through sand and gravel with these rays much as if they were fingers. Whether movement of the prey they disrupt and ingest is detected by these fin rays or by distant touch is not known. Many morphological features of these fishes probably relate to feeding adaptations.

In terms of predators, little is known about predation of the less common species such as the skilfish, but the larger of these bottom-dwelling species tend to be prey to larger fishes (like lingcod) as well as to seals and sea lions. Sablefishes are quite cannibalistic, as are lingcod.

Reproductive biology

Most greenlings, sculpins, and related species lay adhesive masses of eggs that either adhere to rocky substrate, cluster around plant or animal stalks and tubes, or are wedged into crevices. The eggs always adhere to each other, but not always to the spawning substrate. Among the sculpin relatives, only the comephorid sculpins of Lake Baikal give live birth to hatched larvae. Perhaps the most remarkable reproductive specialization among cottoid fishes is the phenomenon of internal gametic association, which has been demonstrated for sculpins (Munehara et al., 1997) and poachers (Munehara, 1997). With internal gametic association, the fishes copulate, but the sperm does not fertilize the egg until introduced to the calcium ions in seawater. This enables a female to repeatedly deposit small egg masses in specific ways over a long period of time, up to dozens or hundreds of depositions over weeks of time, based on one mating. Many highly specialized spawning substrates have evolved in various cottoid species, perhaps on the basis of internal gametic association in more cases than have yet been demonstrated. Proof of internal gametic association merely requires dissection of eggs from ovaries and placement in seawater, then incubation and observation for embryonic development.

Another typical characteristic of sculpin reproduction is the guarding of a cluster of different egg masses by a single territorial male. Male greenlings and lingcod also guard one or more egg masses. In some sculpins, however, the male exhibits haremic behavior in which both the nest site and a group of females are guarded together. In haremic species there is no evidence yet of internal gametic association. With the scalyhead sculpin, *Artedius harringtoni*, this author, while diving, observed several rotund little fish, presumed females, dart inside the empty shell of a giant barnacle, immediately followed by a much larger individual, presumed male, which curled its body and spread its fins to close off entry to the barnacle shell. This species lays its eggs inside giant barnacle shells, and there are typically several different colors of egg mass. Females of various sculpin species lay only one of various characteristic colors of egg. In haremic species of the genus *Artedius*, a cluster of egg masses may number over a dozen masses, but only with a few different colors of egg mass, corresponding to the number of females in the harem. In other genera (e.g. *Scorpaenichthys*, *Enophrys*, *Hemilepidotus*) where the male guards clusters of egg masses of differing colors, it is not known whether haremic behavior is involved, because groups of females have not been observed remaining near the guarding male.

Whereas haremic species tend to lay egg masses that adhere to a rock surface or to previously laid egg masses in a cluster at the guarded nest site, species with internal gametic association tend to lay smaller egg masses of less characteristic size. That is, the female can extrude whatever number of eggs is required to fill an interstitial space or to form a ring around a stalk, then move on to search for another deposition site, the sites being dispersed according to availability. In agonid species there appears to be a tendency to spawn inside sponges, whereas liparidid species tend to spawn in seaweeds or inside shells.

As much as the spawning characteristics vary among sculpins and relatives, their larvae also demonstrate diverse adaptations. Lacking a swimbladder at any stage, these species have evolved diverse mechanisms to enable early growth while inhabiting the water column. Enlarged pectoral fins exist in larvae of many species, whereas larvae of other species have a flaccid, globular body with relatively large volumes of low-density, buoyant body fluid.

Conservation status

Of the families covered in this chapter, the IUCN 2002 Red List includes nine species of the genus *Cottus*: one is categorized as Extinct (*C. echinatus*); two as Critically Endangered; four as Vulnerable; and two as Data Deficient. Sculpins and greenlings tend to inhabit rocky, marine shorelines that are less subject to alteration by human activities than estuarine habitats. For a species like the staghorn sculpin (*Leptocottus armatus*), which uses estuaries as nursery habitat for juveniles, habitat loss can affect populations locally, but the species as a whole is widespread and abundant. For many species that are rarely encountered by people, too little is known of habitat or true abundance to enable determination of conservation status. Where human developments eliminate all natural shoreline, as in municipal harbor areas, intertidal fish species generally lose their natural abundance. It is not known whether greenlings and sculpins are any more sensitive to pollution than other marine fish species. In freshwater lakes and streams, sculpins tend to be depleted both by habitat destruction and by introduction of alien species, as well as by pollution. The widespread distribution of various species of *Cottus* has prevented extinction from occurring at the species level, but geographically significant populations do become threatened.

Only a limited number of these fishes are directly sought in fisheries as food for humans. In the cases of the cabezon (*Scorpaenichthys marmoratus*), the sablefish (*Anoplopoma fimbria*), and the lingcod (*Ophiodon elongatus*), commercial fisheries have led to localized depletion that has necessitated fishing restrictions. In the cases of the cabezon and the lingcod, extended periods of restricted fishing have not led to population recoveries to original levels of abundance. Overexploitation has tended to occur first in more densely populated areas along inland seas and more southerly waters of the Pacific coast of North America.

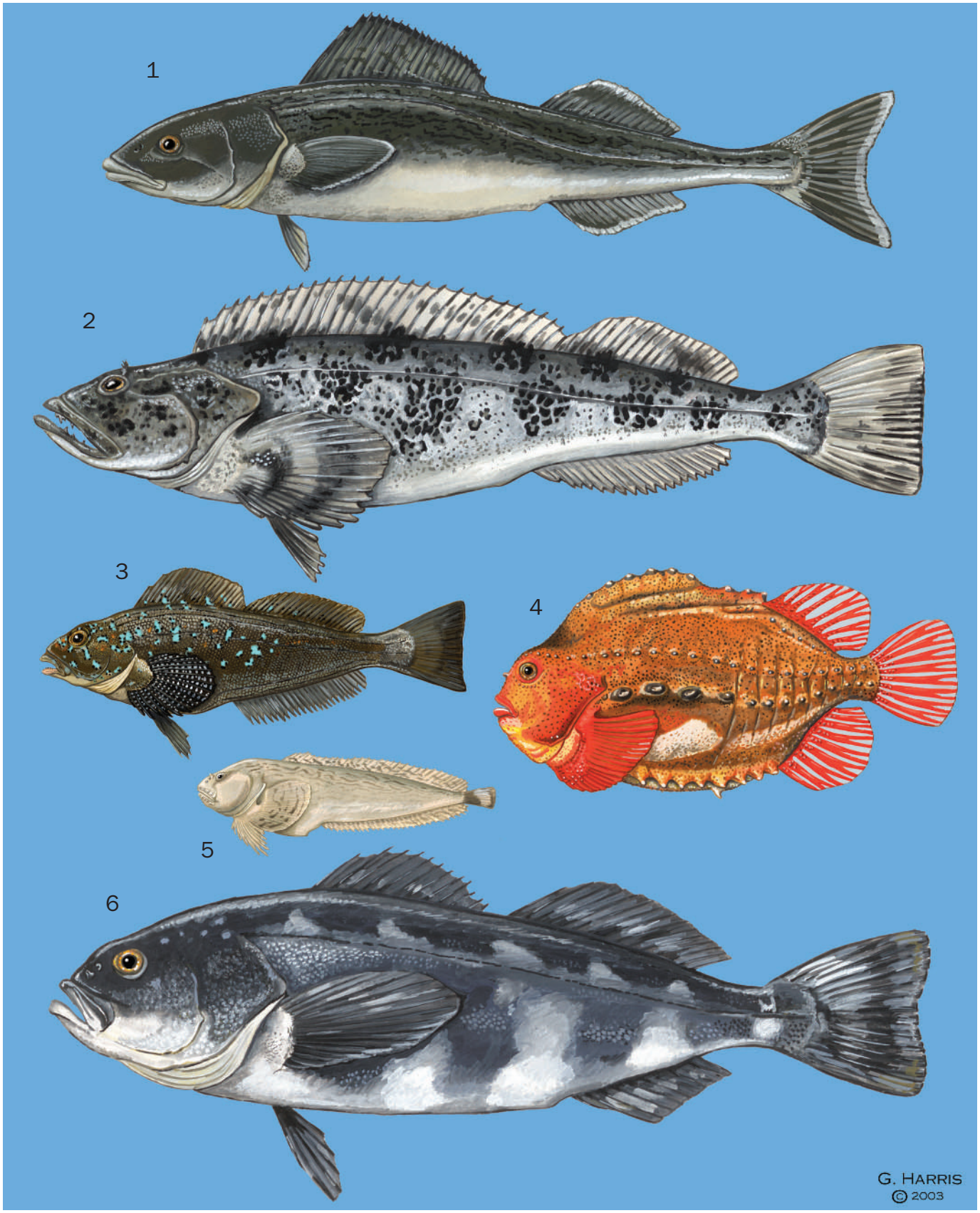
A recent trend in North Pacific fisheries is to land live fishes for Asian markets. The lack of a swimbladder and bottom-dwelling habits render species of greenling and sculpin hardy in this trade. In addition, the head and skeleton are recovered after filleting and used in making soup stock, so that sculpins with large heads are marketable in the live trade. Greenlings and larger sculpins that are of little value in traditional fisheries are becoming increasingly exploited for live seafood trade, owing to the higher prices paid for live fish.

Significance to humans

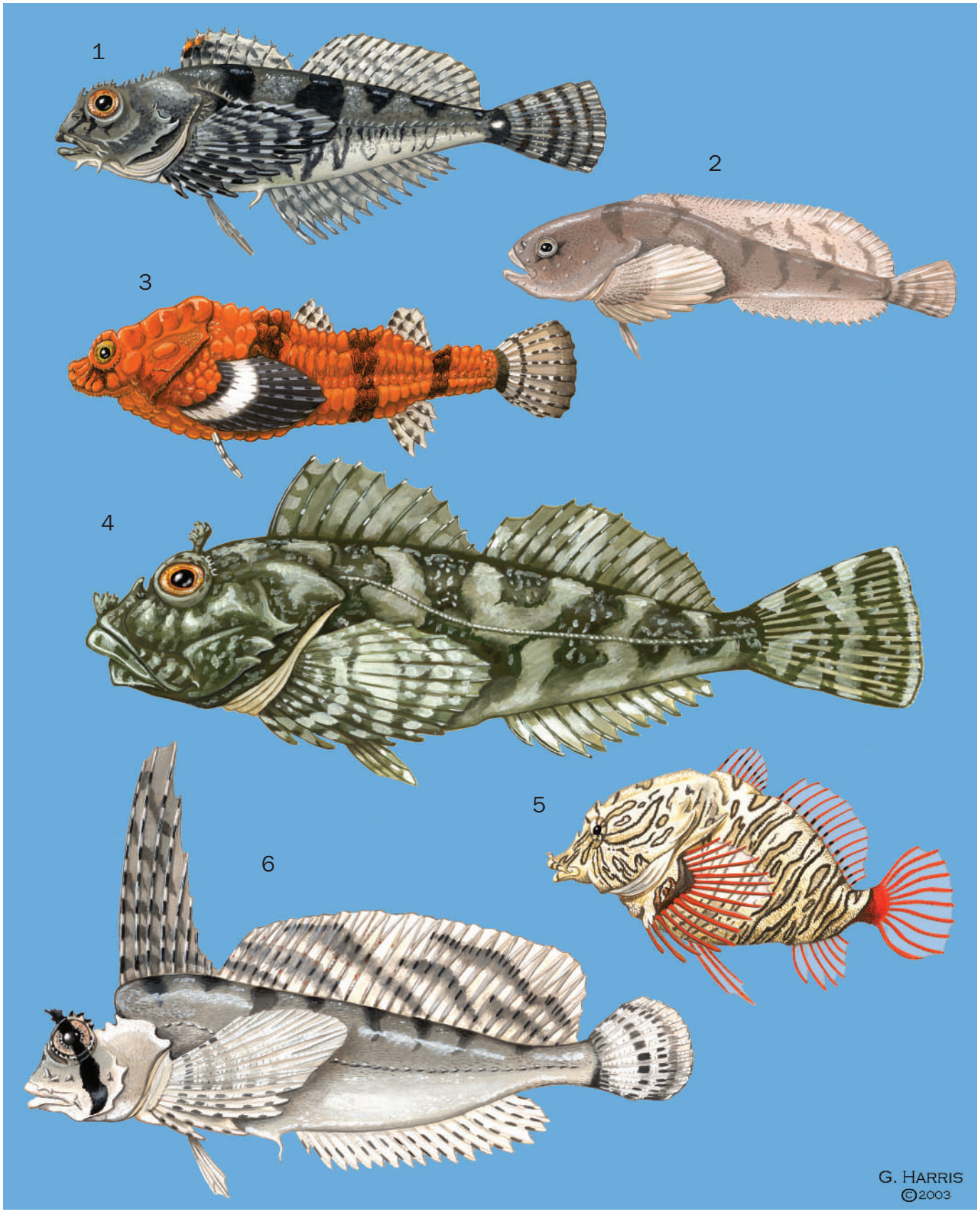
The most obvious significance to humans of greenlings and sculpins is the importance as food of the few commercially sought species. Before the availability of ice or refrigeration systems, the lingcod (*Ophiodon elongatus*) was the target of fishing with hook and line by boats with flooded holds for keeping the fish live (and therefore fresh) until delivery to processing plants. The lack of a swimbladder enabled keeping the lingcod alive during extended fishing trips.

Diversification of fish farming that currently involves salmon species may soon include various relatives of greenlings. The sablefish or Alaska blackcod, *Anoplopoma fimbria*, is the subject of aquaculture research in British Columbia, and at the turn of the millennium the first commercially produced, cultured fingerlings were being grown to market size by salmon farmers.

The unusual body forms of various sculpins and related fishes lends aesthetic value to them. They are popular species for display in public aquariums. Seacoast tourism depends to some extent on the attraction people feel toward exploring tidepools along rocky shores, and intertidal sculpins are among the most readily observed species. Marine biological research has long encompassed study of intertidal sculpins because of their accessibility, and to a similar extent, because of their robust ability to withstand manipulation like tagging or maintenance in aquarium tanks.



1. Sablefish (*Anoplopoma fimbria*); 2. Lingcod (*Ophiodon elongatus*); 3. Breeding male kelp greenling (*Hexagrammos decagrammus*); 4. Breeding male lumpfish (*Cyclopterus lumpus*); 5. Slipskin snailfish (*Liparis fucensis*); 6. Skilfish (*Erilepis zonifer*). (Illustration by Gillian Harris)



1. Tidepool sculpin (*Oligocottus maculosus*); 2. Soft sculpin (*Psychrolutes sigalutes*); 3. Rockhead (*Bothragonus swani*); 4. Cabezon (*Scorpaenichthys marmoratus*); 5. Grunt sculpin (*Rhamphocottus richardsoni*); 6. Sailfin sculpin (*Nautichthys oculofasciatus*). (Illustration by Gillian Harris)

Species accounts

Rockhead
Bothragonus swani

FAMILY
Agonidae

TAXONOMY
Bothragonus swani Steindachner, 1877, previously called *Bothragonus swanii*, Port Townsend, Puget Sound, Washington, United States.

OTHER COMMON NAMES
English: Pithead poacher, pit-headed poacher, pitted poacher, deep-pitted poacher, deep-pitted sea-poacher.

PHYSICAL CHARACTERISTICS
Short, stout body of 3.5 in (9 cm), covered with armor plates and with small fins other than the pectorals. Like other poachers (Agonidae), all fin rays are unbranched, and tail bones are fused. The rockhead, or pithead poacher, is most obvious for its wide, flattened head with a deep indentation in the top. Eyes and mouth are small. As a larva, the pectoral fins become enlarged like butterfly wings, and the body is covered with fine spines. The pelagic juvenile develops heavier, recurved body spines that hook toward the tail. These sharp hooks flatten into armor plates after settlement to the bottom.

DISTRIBUTION
Northern California to Kodiak Island, Alaska.

HABITAT
Rocky shorelines exposed to waves, down to 66 ft (20 m) depth. Found under rocks, in crevices, or among kelp holdfasts.

BEHAVIOR
Very little is known of this elusive fish. When first settled, the hooked body plates serve to prevent the fish from being washed backward by wave surge. It is not known whether the adult braces itself against overhead rock protrusions with the pit in its head. This poacher relies on close hiding quarters and cryptic appearance rather than flight, for predator evasion. If picked up, it vibrates.

FEEDING ECOLOGY AND DIET
Larval rockheads tend to feed on copepods or fish larvae. Adult rockheads feed on small crustaceans.

REPRODUCTIVE BIOLOGY
Orange eggs are deposited within a kelp holdfast. It is not known whether copulation and internal gametic association are required to permit the female to extrude eggs into such interstitial spaces.

CONSERVATION STATUS
Not listed by the IUCN. This poacher is too rarely encountered to permit evaluation, but the exposed, rocky shorelines it inhabits tend not to face human development.

SIGNIFICANCE TO HUMANS
The rockhead is not sought for any purpose and is only rarely displayed in aquariums, since it tends to hide from view. It is poorly studied. ◆

Sablefish
Anoplopoma fimbria

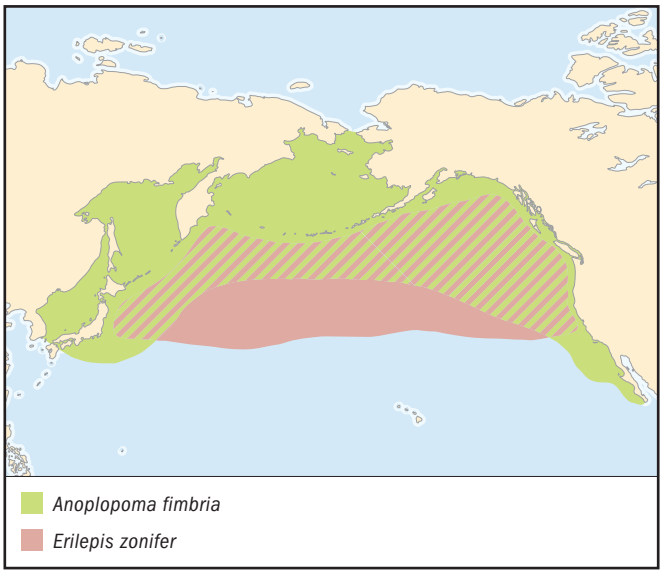
FAMILY
Anoplopomatidae

TAXONOMY
Anoplopoma fimbria Pallas, 1811, San Francisco, United States. Family Anoplopomatidae placed either within suborder Hexagrammoidei or suborder Anoplopomatoidei.

OTHER COMMON NAMES
English: Blackcod, Alaska blackcod, coalfish.

PHYSICAL CHARACTERISTICS
Sablefishes have separate dorsal fins of equal size and a forked tail fin on a streamlined body of gray to black color. Sablefishes grow up to 42 in (107 cm) in length and over 125 lb (57 kg) in weight.

DISTRIBUTION
Deep, offshore waters of the North Pacific, from Baja California (Mexico), to the Bering Sea, and across to southern Japan. Sablefishes range thousands of miles during their lives and occur at depths of over a thousand feet, abundant down to 3,000 ft (914 m). Their young occur in more inshore waters.



HABITAT
Open, deep ocean water of the North Pacific. They often feed near the bottom in association with deep-sea fishes like rattails and grenadiers.

BEHAVIOR
Sablefishes swim at relaxed speeds and approach and school with fishes of other species, sometimes as a prelude to a sideways lunge for a head-first swallowing of the unsuspecting prey. They cannibalize their young when they are abundant in inshore waters.

FEEDING ECOLOGY AND DIET
Sablefishes eat crustaceans, worms, small fishes, and any larger fishes they can capture, which can include salmon almost as long as the sablefish.

REPRODUCTIVE BIOLOGY
Spawning occurs during winter, and the pelagic eggs float in deep water of about 3,000 ft (914 m) where seawater remains constantly cold. Larvae hatch before functional eyes, jaws, or gut have formed and remain deep until absorbing their large yolk. Larvae with large pectoral fins grow in surface waters during spring.

CONSERVATION STATUS
Not listed by the IUCN. Heavily fished through the last century by American, Canadian, Russian, and Japanese longliners and trawlers, sablefishes are now recognized as a depleted species. Catch quotas are now a small fraction of the peak landings that occurred during the middle of the last century. Russian landings from the Bering Sea were reported to have been 38 million pounds (17,000 metric tons) during 1967. Canadian landings at that time were lowest, around one million pounds (454 metric tons).

SIGNIFICANCE TO HUMANS
Sablefishes have been valued greatly as a smoked fish (smoked Alaska blackcod). Their flesh is quite oily. Native North Americans sundried the sablefish. Because they adapt well to living in tanks and net pens, blackcod are being developed as a high-value species for diversification of salmon farms. ◆

Skilfish
Erilepis zonifer

FAMILY
Anoplopomatidae

TAXONOMY
Erilepis zonifer Lockington, 1880, Monterey, California, United States. This species is sometimes placed alone in the family Erilepidae in the suborder Anoplopomatoidei, but the more accepted classification puts them together with sablefishes in the Anoplopomatidae and within the Hexagrammoidei.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The largest of the greenlings and sculpins, skilfishes resemble a heavier version of a sablefish with mottled blue of dark and light shades. Older fishes reach 70 in (178 cm) length and 200 lb (91 kg) weight.

DISTRIBUTION
Deep water of the North Pacific from Monterey Bay, California, to central Honshu Island, Japan and north to the Gulf of Alaska and Kamchatka.

HABITAT
Young are sometimes caught in offshore, surface waters. Adults are typically caught in deeper water.

BEHAVIOR
Not known.

FEEDING ECOLOGY AND DIET
Not known.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Not listed by the IUCN. Little is known of the behavior, food habits, or reproduction of this species. It is not the subject of directed fisheries, so there is little basis for determining whether incidental bycatch in other high seas fisheries might have detrimental impact upon the abundance of the skilfish.

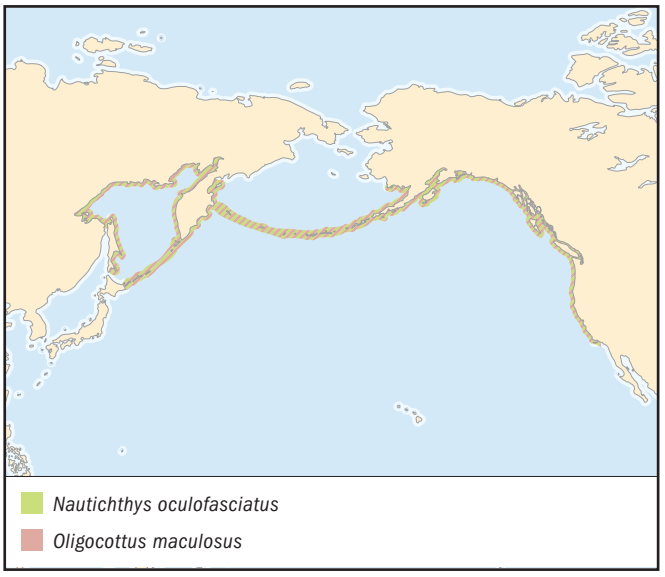
SIGNIFICANCE TO HUMANS
None known. ◆

Sailfin sculpin
Nautichthys oculofasciatus

FAMILY
Cottidae

TAXONOMY
Nautichthys oculofasciatus Girard, 1857, Fort Steilacoom, Puget Sound, Washington, United States. Has been listed as *Nautichthys oculo-fasciatus* and has been segregated from the Cottidae into the family Hemitripteridae on the basis of scales modified into embedded spines.

OTHER COMMON NAMES
English: Sailor fish.



PHYSICAL CHARACTERISTICS
The elongated rays of the first dorsal fin and the long second dorsal and anal fins, together with a dark bar through the eye joining a dark flap of skin over each eye, cause the cream or brown sailfin sculpin to appear very cryptic, especially among seaweed. Sailfins reach 8 in (20 cm).

DISTRIBUTION
From southern California to the Sea of Okhotsk.

HABITAT
Sailfins live on rocky reefs and outcroppings, and on adjacent sand bottom, from shallow water down to over 360 ft (110 m) depth.

BEHAVIOR
In shallow water, the sailfin sculpin waves its first dorsal fin back and forth in synchrony with the motion of adjacent seaweeds in the surge. Between waves of the dorsal fin, the sailfin hops forward by rippling the second dorsal fin and sculling with the pectoral fins. In captivity, sailfins that have never experienced any surge perform the same combination of hopping forward between sweeps of the first dorsal fin. This disruptive mimicry of seaweed obscures the movement of the fish and may enable close approach to prey. This species is nocturnally active.

FEEDING ECOLOGY AND DIET
Feeds on small shrimps and other crustaceans. Individuals slowly approach their prey prior to hopping forward and engulfing them.

REPRODUCTIVE BIOLOGY
Sailfin sculpins copulate, and internal gametic association enables the female to repeatedly extrude the bright orange eggs into interstitial spaces among mussels in the intertidal over a period of weeks during winter. The female must migrate into shallow water during high tides in order to reach the mussel beds, where the eggs are periodically exposed to air but are kept cool and damp by the mussels. Larval sailfin sculpins develop extremely elongate pectoral fins that are spread like butterfly wings and used to glide down through the water column while the larva forages on zooplankton. This behavior enables sailfin sculpins to reach relatively large sizes before permanently settling during late spring.

CONSERVATION STATUS
Not listed by the IUCN. Elimination of mussel beds by harvesting or pollution will limit the reproduction of the sailfin sculpin, but the small fish is not directly taken for any purpose other than use in aquarium displays. As with the grunt sculpin, larvae of the sailfin sculpin are easily cultured.

SIGNIFICANCE TO HUMANS
Sailfin sculpins are popular with night divers and as display species in public aquariums. ◆

Tidepool sculpin
Oligocottus maculosus

FAMILY
Cottidae

TAXONOMY
Oligocottus maculosus Girard, 1856, Neah Bay, Washington, United States.

OTHER COMMON NAMES
English: Tidepool johnny.

PHYSICAL CHARACTERISTICS
Typical sculpin body form, with a small, elongate body, to 2 in (5.1 cm), and a relatively large head. Tidepool sculpins have varying numbers and sizes of cirri on their body, singly or in pairs, especially in the head region. They have one forked cheek spine. Color is banded light and dark gray, sometimes with red or green shades. Newly settled young have red fin rays on the tail.

DISTRIBUTION
Coastal waters from the Los Angeles Bight to the Bering Sea and the Sea of Okhotsk.

HABITAT
Many scientific studies of tidepool sculpins living in tidepools have led to the opinion that this species is an obligate dweller of tidepools. Ironically, spawning is much more dense in protected areas without tidepools than on exposed headlands where pools are formed. Furthermore, tidepool sculpins are abundant in inlets where no tidepools occur, and they strand under rocks during low tides in areas without tidepools. Thus, the tidepool sculpin is a facultative inhabitant of tidepools where they occur, but does not require them to make a living.

BEHAVIOR
When it occurs in tidepools, the tidepool sculpin exhibits homing behavior when displaced from a home pool. The sense of smell appears to assist in home site recognition.

FEEDING ECOLOGY AND DIET
Small crustaceans like amphipods or harpacticoid copepods.

REPRODUCTIVE BIOLOGY
Although it is not known whether this species has internal gametic association, the female mates and then deposits egg clusters in spaces between barnacles or mussels. The eggs are either emerald green, dark green, or maroon. Maroon eggs are laid on shores exposed to wave action, but the same females, removed from exposed shores, in captivity lay green eggs the next season. On small stretches of shore that either gradate or abruptly shift from wave exposure to protection from waves,

the proportion of maroon to emerald eggs similarly gradates or shifts abruptly. The egg pigment may reflect some physiological response of the female to the gas saturation of the seawater, but the subject remains a mystery, as does the polymorphism for egg color in many other sculpin species.

CONSERVATION STATUS
Not threatened. This is the most abundant and commonly occurring shoreline fish in many parts of the Pacific Northwest. It would probably be one of the last species to disappear in the face of environmental degradation.

SIGNIFICANCE TO HUMANS
The tidepool sculpin is the most easily observed fish in many tidepools, and it has been of great interest to students of intertidal biology. ◆

Grunt sculpin
Rhamphocottus richardsoni

FAMILY
Cottidae

TAXONOMY
Rhamphocottus richardsoni Günther, 1874, Fort Rupert, western North America (Prince Rupert, British Columbia, Canada). Sometimes classified alone in the family Rhamphocottidae.

OTHER COMMON NAMES
English: Grunt-fish, pigfish.

PHYSICAL CHARACTERISTICS
With a short, stout body and a large head with elongate snout, the resemblance of a grunt sculpin to a pig is only enhanced by the way it uses its large pectoral fins to scoot around on the seabed. The lower rays of the pectoral fin are elongate and have almost no webbing. The body is covered with small, bristly spines. All of the fin rays are unbranched and the tail bones are fused, as in poachers (Agonidae). These fish grow to 3.3 in (8.3 cm).

DISTRIBUTION
From Santa Barbara, California, to the Bering Sea coast of Alaska.

HABITAT
Occurs in shallow coastal waters down to 660 ft (200 m) depth, on rocky or shell/sand bottoms, often associated with encrusting invertebrates like giant barnacles.

BEHAVIOR
The elongate pectoral rays can function like fingers for crawling over coarse surfaces. Grunt sculpins are more frequently observed walking over the seabed than swimming. They hide in empty barnacle shells and may appear to be mimicking live barnacles.

FEEDING ECOLOGY AND DIET
Video analysis of predation by grunt sculpins reveals a highly adapted method of capturing relatively large shrimp by approaching obliquely, then snapping the head sideways while extending the snout and sucking water in together with the prey.

REPRODUCTIVE BIOLOGY
Nesting often occurs inside barnacle shells, and controversy exists over whether the female or the male tends the eggs, or whether a mated pair trade off guarding duties. Parental care includes assisting hatching, the parent sucking out hatchlings and spitting them upward into the water. A young female spawns a single mass of eggs in late winter or spring, but with increasing age the females start reproducing with increasing frequency until, at a decade of age, captive females reproduce year-round.

CONSERVATION STATUS
Not listed by the IUCN. The only conservation concern relates to possible temporary depletion at popular diving reefs by past collections for display aquariums. Grunt sculpins are easily cultured, however, and most specimens for public display are now propagated in laboratories at major aquariums.

SIGNIFICANCE TO HUMANS
The grunt sculpin is a popular quarry of scuba divers on rocky reefs along the Pacific Northwest. Similarly, they are popular for display in aquariums because of their unusual appearance and interesting habits. ◆

Cabezon
Scorpaenichthys marmoratus

FAMILY
Cottidae

TAXONOMY
Scorpaenichthys marmoratus Ayres, 1854, San Francisco, California, United States. Has at times been separated into its own family, Scorpaenichthyidae.

OTHER COMMON NAMES
English: Giant marbled sculpin, giant sculpin.

PHYSICAL CHARACTERISTICS
This relatively huge fish (to 30 in [76 cm] and 30 lb [13.6 kg]) has a marbled color pattern that incorporates light and dark gray, brown and beige, or olive green shades. The young often have shades of red. Scales are covered by skin. This is the only sculpin with an unpaired flap of skin on the tip of the snout. The pelagic juvenile is metallic blue, shaped like a blunt-nosed, short salmon smolt.

DISTRIBUTION
Central Baja California, Mexico, to Sitka, southeast Alaska.

HABITAT
Inhabits rocky reefs from very shallow depths down to the limits of kelp growth, sometimes deeper. They tend to hide in kelp beds, sometimes literally hanging in the seaweed. Juveniles occur in tidepools.

BEHAVIOR
An ambush predator, the cabezon tends to be sedentary, relying on the camouflage of its coloring. If stranded in kelp during low tide, a cabezon flares its gill covers and holds still. Pelagic juveniles are attracted to turbulence in a laboratory situation, and will strike at prey in the most rapid flows they can find, which may lead them to settle on exposed shorelines.

FEEDING ECOLOGY AND DIET
Kelp crabs, other crabs, shrimp, snails, clams, worms, or small fish.

REPRODUCTIVE BIOLOGY
Males guard clusters of egg masses during late winter and spring. The egg masses vary in color from burgundy to purple to dark green. The eggs are toxic to birds and mammals that might otherwise predate on them during low tide exposure. Small sculpins crowd in to predate on cabezon larvae hatching at the edges of the nest site, without the male paying any attention to their activity.

CONSERVATION STATUS
Not listed by the IUCN. Cabezons show signs of being overfished through their southern range. Depletion is evident in southern British Columbia, where they are not the target of either sport or commercial fishing, although bycatch landings occur in both fisheries. Commercial setline fishing has been directed at cabezons in California for over half a century, and they are considered a top sport angling species there as well. Cabezon spearfishing is popular because of the ease of spearing these big fish.

SIGNIFICANCE TO HUMANS
The firm flesh of the cabezon is favored by many. It is a popular sport fish with bait anglers, especially in California. ◆

Lumpfish
Cyclopterus lumpus

FAMILY
Cyclopteridae

TAXONOMY
Cyclopterus lumpus Linnaeus, 1758, Baltic Sea and North Sea.

OTHER COMMON NAMES
English: Henfish, lumpsucker; French: Grosse poule de mer.

PHYSICAL CHARACTERISTICS
Thick body with rows of hard, conical tubercles, and with a soft, cartilaginous hump on the back, embedding the first dorsal fin. The tubercles are in a single row along the back and in three lateral rows on each side. Pelvic fins are modified into a suction disc. The fish is green, gray, blue, or brown, with red highlights on breeding males. Breeding females become distended with eggs. Lumpfishes have reached 2 ft (61 cm) and 21 lb (9.5 kg).

DISTRIBUTION
Across the North Atlantic Ocean from Chesapeake Bay to Hudson Bay, Greenland, Iceland, the White Sea, and south through the British Isles to France.

HABITAT
This is a bottom fish that inhabits cold waters on rock bottom. Early in life the hatchlings, fully formed as juveniles, are in surface waters, then older juveniles are semipelagic, living under seaweed.

BEHAVIOR
From the time of hatching, lumpfishes are capable of using their pelvic sucking disc to adhere to smooth surfaces, which tend first to be seaweed blades, then rocks.

FEEDING ECOLOGY AND DIET
Crustacean plankton like krill, amphipods, and copepods, as well as jellyfishes and small fishes.

REPRODUCTIVE BIOLOGY
Early in spring the lumpfish female deposits an adhesive egg mass of over 100,000 eggs on rocky bottom among seaweed. Lumpfishes spawn more than one batch of eggs, and hatching occurs from May to July, after six to ten weeks of incubation. Egg color is polymorphic between different females, including colors like brown, red, pink, orange, yellow, green, and purple.

CONSERVATION STATUS
Not listed by the IUCN. Early accounts listed the lumpfish as being of no economic value, but they were always a bycatch in

the inshore cod trap and gillnet fishery, and their ripe eggs were marketed as caviar starting in the late 1960s. In North America the flesh is sold as dog food, but it is eaten by people in Europe. The eggs are stripped from ripe females and packed in brine for preparation as lumpfish caviar.

Overfishing has occurred. In Newfoundland the catch rate was 229 lb (104 kg) per net per year in 1979 (total landings 85 tonnes) at 16 nets per boat, whereas by 1996 the catch rate was down to 21 lb (9.5 kg) per net per year (total landings still 82 tonnes) at 40 nets per boat, and nearly ten times as many boats in the same region.

SIGNIFICANCE TO HUMANS
With the decline of beluga sturgeon and other traditional sources of caviar, lumpfish caviar has become highly valued. ◆

Kelp greenling
Hexagrammos decagrammus

FAMILY
Hexagrammidae

TAXONOMY
Hexagrammos decagrammus Pallas, 1810, formerly *Chiropsis decagrammus* Pallas, Cape St. Elias, Alaska, United States.

OTHER COMMON NAMES
English: Tommy cod, speckled sea trout, greenling sea trout.

PHYSICAL CHARACTERISTICS
Reaches 24 in (61 cm), 4.6 lb (2.1 kg), males smaller. Five lateral lines occur along each side of body, and the male is blue-brown with prominent light blue spots on top of head and anterior body; the female is yellow-brown with small red or orange spots.

DISTRIBUTION
Santa Monica Bay, southern California, to Amchitka Island (Aleutians), Alaska.

HABITAT
Inhabits shallow, subtidal seabed on rocky shores, often around kelp beds.

BEHAVIOR
Fairly active; males in particular cruise around a home area during daylight. More aggressive than the whitespotted greenling, *Hexagrammos stelleri*, which sometimes cohabits with kelp greenlings, the kelp greenling even feeds on unguarded lingcod eggs.

FEEDING ECOLOGY AND DIET
Small shrimps as well as worms and small fishes.

REPRODUCTIVE BIOLOGY
Courtship occurs in late fall, with spawning from October through December, eggs hatching in January through February. The male guards the nest site, at which successive females will be courted for spawn deposition. Eggs are blue to purple with a pale center when first laid, becoming golden brown when embryos are eyed. Larval and pelagic juvenile stages last about two months, with these early stages a gun barrel blue, with snub snout shape. Juveniles school over rock faces prior to settlement and metamorphosis to a benthic juvenile resembling the adult. Sexually dimorphic color is evident during the first summer.

CONSERVATION STATUS
Not listed by the IUCN. Kelp greenlings are caught as bycatch in hook and line fisheries for live rockfishes, and have achieved their own localized market demand in Asian communities in Vancouver, Seattle, San Francisco, and Los Angeles. Little potential exists for overharvest by sport anglers unless using small tackle, owing to small mouth size. Serious depletion of larger groundfish species could prelude the depletion of greenlings in a localized area, since hook, live market, and line fishery includes landings of greenlings as well as larger groundfishes.

SIGNIFICANCE TO HUMANS
Fillets of kelp greenling are high quality. Kelp greenlings are desired in the retail marketing of live fish (primarily rockfishes). Kelp greenlings are too small to provide enjoyable sport fishing unless light tackle is used, but greenlings are easy to catch and therefore provide good sport for small children. ◆

Lingcod
Ophiodon elongatus

FAMILY
Hexagrammidae

TAXONOMY
Ophiodon elongatus Girard, 1854, San Francisco, California, United States. Sometimes placed in family Ophiodontidae.

OTHER COMMON NAMES
English: Cultus cod, ling.

PHYSICAL CHARACTERISTICS
Lingcod are large, up to 5 ft (1.5 m) in length and 100 lb (45 kg) weight (males smaller), and have a large mouth extending

behind the eyes. The mouth has prominent teeth. The spiny and soft dorsal fins are joined to form one long, moderately notched dorsal fin running the entire length of the body behind the head, and the tail fin is squared, not forked. The color is brown, rarely blue-green, with a staggered array of black blotches along the body midline and top.

DISTRIBUTION
From Ensenada, Mexico (Baja California), to the Alaska Peninsula (Shumigan Islands).

HABITAT
Lingcod spawn on rocky reefs along the shoreline, usually at depths of about 33–99 ft (10–30 m), but spawning has been observed in the intertidal and by submarine at much greater depths. The females migrate onto sand and mud bottoms at greater depths up to 330 ft or more (100 m), except when they return inshore for spawning, whereas males tend to remain all year on the spawning reefs. Lingcod will hide in crevices. Young lingcod tend to be more generally distributed near the shoreline, avoiding areas occupied by adults. Recently settled lingcod have been collected in eelgrass beds and have been seen from a submarine on flat bottom at the base of a cliff over 360 ft (110 m) deep.

BEHAVIOR
Aside from male territoriality, female seasonal migrations, and rapacious predatory behavior, lingcod tend to be sedentary ambush predators. They rest near rocks and wait for prey to swim near. During salmon migrations, however, lingcod have been observed predating at the surface over great depths, so relative abundance and position of prey affect behavior.

The life history of lingcod relates closely to that of Pacific herring. Larval lingcod settle from the plankton at the time during spring when herring larvae are becoming silver juveniles. Young lingcod that have not settled permanently from a swimming habit search in school formation during the twilight hours of dawn and dusk, and young herring are their favorite prey.

FEEDING ECOLOGY AND DIET
Although lingcod will eat invertebrates such as crabs, shrimps, and octopi, they mainly feed on other fishes, including younger lingcod. A lingcod engulfs another fish head-first. The throat rapidly opens while the mouth engulfs the prey, so that a fish about two-thirds the length of the lingcod will be swallowed immediately into the entire length of the stomach, with only the tail protruding from the mouth. During years of abundant prey, growth is rapid. After two years lingcod of both sexes tend to reach about 1.5 ft (46 cm) in length, after which males grow more slowly than females, perhaps owing to the seasonal feeding migration that only females undertake.

REPRODUCTIVE BIOLOGY
Males become jet black and fight over territory during winter, prior to arrival of ripening females. Males will successively spawn with different females, guarding up to three egg masses at a time. Males are capable of spawning at two years of age, and females at three, but most females do not lay eggs until they are four. If larger females are not abundant, then females tend to mature and spawn a very small egg mass at three years of age. In British Columbia, peak abundance of guarded egg masses is during February, although spawning can occur from December through April. Spawning occurs later in more northerly latitudes. Older females of 10–15 years of age can spawn a half million eggs, and they spawn earlier and deeper than the younger fish. Larvae spawned by the largest females tend to be slightly larger than larvae of small females, which could confer advantage under certain feeding conditions in the plankton. Thus, a population with a full demographic spread from young to old fish will have greater chances of survival of young under a variety of environmental conditions.

CONSERVATION STATUS
Not listed by the IUCN. Lingcod have been extremely depleted since the 1980s in Puget Sound, and since the 1990s in the Strait of Georgia. Outer coast populations have become overfished in more recent years. It has been demonstrated mathematically that even the earliest hand-line fisheries prior to World War II led to significant reduction in lingcod biomass in inland seas around Vancouver and Seattle. More efficient otter trawls in the 1940s greatly increased levels of landings, which in British Columbia exceeded eight million pounds per year (over 3,700 metric tons). Landings in the Strait of Georgia were negligible when the commercial fishery closed in 1990, but since then it has become evident that sport fishing alone can prevent population recovery near metropolitan areas. Lingcod are of interest for management strategies that include protection within sanctuaries (marine protected areas).

SIGNIFICANCE TO HUMANS
The common name "cultus" is a Coast Salish term meaning "cheap," which indicates that original levels of abundance ensured that lingcod could be caught for use as food when preferred species like halibut became less available. As mentioned, lingcod has always been valued as a fresh fish. Aquaculture is possible but not yet economical. Appreciation of the value of lingcod as a sport species tends to increase as the availability of this and other groundfish species declines in a given area. ◆

Slipskin snailfish
Liparis fucensis

FAMILY
Liparididae

TAXONOMY
Liparis fucensis Gilbert, 1895, Strait of Juan de Fuca, 109 fathoms. Is classified sometimes within the Cyclopteridae, and the family name Liparididae was formerly Liparidae.

OTHER COMMON NAMES
English: Juan de Fuca liparid.

PHYSICAL CHARACTERISTICS
This snailfish grows to 7 in (18 cm) and has a lobe at the front of its dorsal fin and the anal fin barely extending onto the tail fin. Color is from brown to olive. Like other snailfish, it has a tadpole shape to the body, large pectoral fins with extended lower rays, and a small pelvic suction disc. Larvae become spherical in a globular bubble of body fluid beneath the skin. Immediately upon settlement there is a metamorphic change (shrinkage) to a snailfish shape like a tadpole.

DISTRIBUTION
Northern California to southeast Alaska.

HABITAT
Has been collected over a wide range of depths from the shore down to 1,270 ft (388 m).

BEHAVIOR
The larval stage grows for an extended period in the planktonic realm by means of neutral buoyancy conferred by the globby, bubble shape of the body.

FEEDING ECOLOGY AND DIET
Small crustaceans including shrimp.

REPRODUCTIVE BIOLOGY
The male slipskin snailfish guards a cluster of egg masses inside an empty mussel shell during spring. Egg color varies between egg masses, from tan to pink or orange.

CONSERVATION STATUS
Not listed by the IUCN. This snailfish is relatively common in occurrence.

SIGNIFICANCE TO HUMANS
None known. ◆

Soft sculpin
Psychrolutes sigalutes

FAMILY
Psychrolutidae

TAXONOMY
Psychrolutes sigalutes Jordan and Starks, 1895, Puget Sound near Port Orchard, Washington, United States. Species is listed as *Gilbertidia sigalutes* in older species compendiums, and is listed as a member of the family Cottidae.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The soft sculpin has flaccid skin in which the single dorsal fin seems embedded. The lateral line and head canal pores of adults are large and obvious, especially around the jaws and cheeks. Adults are dark brown or translucent beige. Adult males are much larger than females and often have scars over their large heads. Males can approach 3.5 in (9 cm) in length. The pelagic young have relatively larger eyes, no obvious pores, and are purple with orange pectoral fins.

DISTRIBUTION
Coastal waters from Puget Sound, Washington, to the Aleutian Islands, Alaska.

HABITAT
Larvae of the soft sculpin migrate to feed at the surface at dawn and dusk. Then as pelagic juveniles, they alternate between settling to soft bottom and migrating to the surface on dark nights when surface plankton is abundant. Females grow to 75% of mature body size while exploiting the plankton. Soft sculpins permanently settle during late spring and occupy deep crevices or recesses in multilayered rock rubble, usually on shorelines protected from wave surge.

BEHAVIOR
The male soft sculpin continues growing after settlement, whereas the female starts developing ripe ovaries. The male is highly territorial, rotating his body in a circle and stuttering his head to keep other males away from his territory. Head biting occurs among males.

FEEDING ECOLOGY AND DIET
Feeding is visual during early larval stages, then the pelagic juveniles switch to use of distant touch at night as the eyes become relatively smaller and the head canal pores enlarge. Adults in crevices use distant touch to detect crustacean prey like amphipods. Adults cannibalize young soft sculpins that enter their territory.

REPRODUCTIVE BIOLOGY
The male soft sculpin attracts a harem of several females and courts them in synchrony prior to copulating with each female in sequence. Females simultaneously lay a group, monolayer egg mass on the underside of a rock surface. The females tend the eggs communally, the fanning behavior of one female stimulating similar behavior in adjacent females. The male remains to one side and guards the nest site against other fishes or invertebrates. At hatching, the females suck larvae from the egg shells, swim away from the nest crevice, and spit the larvae toward the surface.

CONSERVATION STATUS
Not listed by the IUCN. Detection of soft sculpins tends to occur rarely. It is doubtful whether human activities directly affect this species.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

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Jeffrey Burton Marliave, PhD

Percoidei I

(Perches and darters, North American basses and sunfishes, pygmy sunfishes, and temperate basses)

Class Actinopterygii
Order Perciformes
Suborder Percoidei
Number of families 4

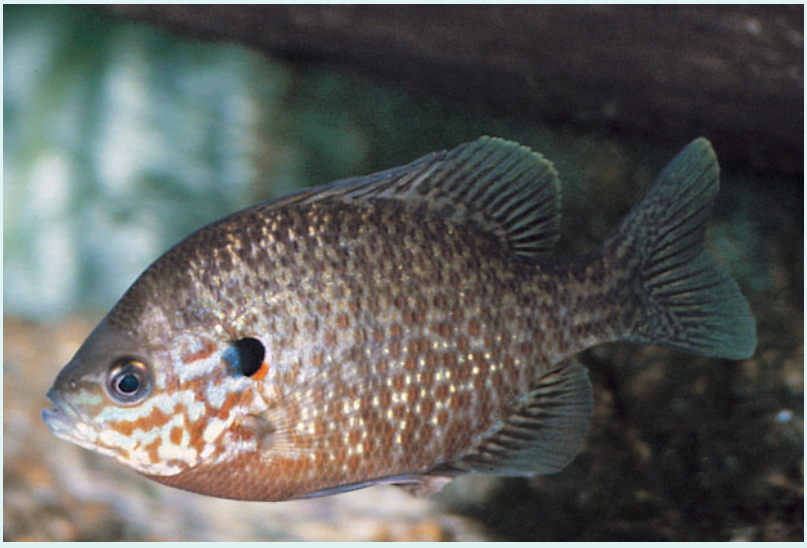


Photo: The pumpkinseed sunfish (*Lepomis gibbosus*) is found in large numbers in the shallow sheltered areas of ponds and lakes. (Photo by Animals Animals ©Stouffer Prod. Reproduced by permission.)

Evolution and systematics

The suborder Percoidei contains more than 70 families and 2,800 species. This chapter and the four Percoidei chapters that follow highlight a representative sample of Percoidei taxa. This chapter focuses on four families:

- Percidae, the perches, with 10 genera and 162 species
- Centrarchidae, the sunfishes, with eight genera and 29 species
- Elassomatidae, the pygmy sunfishes, with one genus and six species
- Moronidae, often grouped under the umbrella descriptor "temperate basses," with two genera and six species

All four families fall within the massive order Perciformes, although the placement of Elassomatidae in this order has been disputed. The current classification positions Percidae, Centrarchidae, and Moronidae within the 71-family suborder Percoidei, and the pygmy sunfishes in the single-family suborder, Elassomatoidei. Some taxonomists have suggested moving the elassomatids out of the percomorphs altogether and placing them into the atherinomorphs, a broad grouping that includes the killifishes (cyprinodonts), but at least one genetic analysis (Jones and Quattro, 1999) discounts this change. Past arrangements had placed the pygmy sunfishes together as a subfamily within Centrarchidae, but their similarities in appearance have since been attributed to evolutionary convergence.

Changes have also occurred in other families. The moronids, for example, now include species formerly within the family Percichthyidae. Some biologists consider them to be most closely related to the snooks and giant perches in the family Centropomidae, because both share two additional lateral lines on the tail, above and below the main lateral line. Little doubt exists that all four families—Percidae, Centrarchidae, Moronidae, and Elassomatidae—will undergo further taxonomic alterations in the future, as scientists learn more about the phylogenetic relationships between species, genera, and higher classifications.

Physical characteristics

The perch family is a large one, making generalizations about physical appearance rather difficult. These species do, however, have some unifying traits, such as an elongate body. All percids except the genus *Zingel* have either two fully separate dorsal fins or two dorsal fins that are only minimally connected. The opercle has one sharp spine. Most fishes in this family, including the North American darters, are on the small side. One exception is the walleye (*Stizostedion vitreum*), a popular game fish that can grow to 42 in (107 cm).

Sunfishes, many of which are described by the angler simply as "panfish," are typically broad animals with bodies one-third to one-half as tall as they are long. The single dorsal fin usually has 10–12 spines, although the range runs from 5–13. Some, like the longear (*Lepomis megalotis*) and pumpkinseed sunfishes (*L. gibbosus*), are colorful in hues of orange, green, and blue, while others are quite drab. Maximum adult sizes range from less than 4 in (10 cm) in two *Enneacanthus* species, to 39 in (nearly 1 m) in the largemouth bass (*Micropterus salmoides*).

Moronid species all have two dorsal fins, including a spiny front fin and a mostly soft-rayed hind fin. Other distinguishing

Male *Elassoma okefenokee* in full breeding color. (Illustration by Michelle Meneghini)

features include a two-spined opercle and a long lateral line with two additional lateral lines on the tail. Maximum adult sizes range from nearly 1.5 ft (46 cm) in the white bass (*Morone chrysops*), to 6.6 ft (2 m) in the striped sea bass (*M. saxatilis*).

Members of the pygmy sunfish family have a rounded tail fin and a three- to five-spined dorsal fin with eight to 13 soft rays. They lack a lateral line on the body. Pygmy sunfishes are less broad than the typical centrarchid and considerably smaller. Maximum adult sizes range from 1.3 in (3.3 cm) in the Carolina pygmy sunfish (*Elassoma boehlkei*), to 1.9 in (4.7 cm) in the banded pygmy sunfish (*E. zonatum*).

Sunfish nests. (Illustration by Emily Damstra)

Distribution

Most species in this group occur in North America. Some percid species extend throughout the Northern Hemisphere, and the family Moronidae contains members that naturally occur in Europe and northern Africa. In addition to the native populations of the four families, numerous species, particularly among the centrarchids and percids, have been purposely introduced as game and/or food fishes in new geographic areas nearly around the world. As a result, various centrarchid species are now found in lakes and ponds throughout temperate Europe, Japan, and southern Africa and Australia.

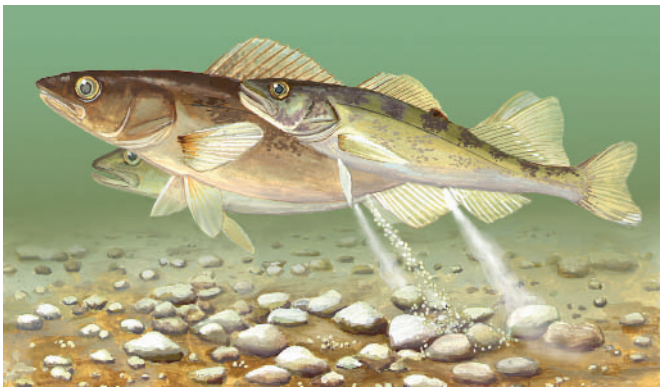
Habitat

Fishes in the families Centrarchidae and Elassomatidae live in strictly freshwater habitats. Centrarchids prefer a temperate climate, and are especially common to lakes, streams, and other inland waterways in the northern United States and Canada. Many seek out weedy areas or other protective cover, such as swamps with fallen trees. Elassomatids similarly inhabit swampy areas with heavy vegetation, but favor the warmer environs of the southeastern United States.

The large family Percidae is primarily a freshwater group, with species in just about every type of waters, from lakes and swamps to both fast- and slow-moving streams and other bodies of water. Some live in the brackish waters of estuaries and in salt lakes. Moronids are the most versatile of the four families in regard to habitat, with members existing in fresh, brackish, and marine waters along coasts.

Various species within these families may coexist in a single body of water. For example, a typical inland lake in the Great Lakes region may be home to numerous species, including largemouth bass, bluegill (*Lepomis macrochirus*), and

Largemouth bass (*Micropterus salmoides*) cleaning the eggs in its nest. (Illustration by Emily Damstra)



Two males and one female (large, center fish) walleye (*Stizostedion vitreum*) spawning. (Illustration by Emily Damstra)

others in the family Centrarchidae, as well as the yellow perch (*Perca flavescens*), walleye, and others in the Percidae.

Behavior

Because of the breadth of this four-family group, behavior varies widely. Some species school; some exist alone. Some are broadcast spawners; others build nests and mate one-on-one. Numerous species provide no parental care; others build nests and guard eggs and/or young.

The centrarchids are particularly known for their nest-building and parental care. Nest-building typically involves the male setting up a small territory, fanning its tail to create a depression in the substrate, then enticing a receptive female to his nest to lay her eggs, which he fertilizes. In many centrarchids, as well as darter perches, more than one female may be attracted to a male's territory. This often results in the male mating with different females in a single breeding season. Male centrarchids defend the nest at least until the eggs hatch, and the males of a few species continue to watch over the young for several weeks.

One unusual behavior has gained some attention. Largemouth bass in the family Centrarchidae will frequently eat whirligig beetles (*Dineutes hornii*), which are flat, round insects that move along calm water surfaces in looping, swirling patterns. These beetles secrete a noxious slime that repels most predators. The bass, however, have developed a way to get around the goo. According to researchers, they rinse off the beetle by repeatedly taking the insect into the mouth, gargling it, and spitting it out until the unpleasant taste is gone, or until the bass gives up. If the bass is persistent enough to rinse off the slime (which can take more than a minute) it eats the beetle. If not, the beetle escapes.

The darters comprise a huge group within the perch family, and the 146 species live in waters of North America. Members are characterized by their wary nature: Whenever the slightest threat arises, they quickly "dart" for cover. They also exhibit other interesting behaviors. The johnny darter (*Etheostoma nigrum*), for instance, has atypical spawning habits. The male prepares a spot under some cover, perhaps a rock overhang. When a mate arrives, the male and female both swim to the site and turn upside down to spawn. The female's eggs stick to the overhead cover. The male's job is to tend and guard the eggs for the next several weeks until they hatch. Other fishes in the Percidae may mate in pairs like the johnny darter, spawn in small assemblages of one female and several males, or engage in mass spawning.

The breeding season for moronids begins with male courtship displays, usually involving one female and several males. The routine typically includes the males closely following a female and nudging her vent area, and in some species, stereotypically swimming in circles. When appropriately stimulated, the female rises to the surface with the males in tow, and spawning occurs. Occasionally, some *Morone* species will hybridize with each other.

Perhaps the most interesting behavior among the elassomatids occurs during territorial and courtship displays. The territorial display takes place when a male approaches another's territory. The territorial male displays toward the intruder by expanding and/or rapidly flitting his fins, turning sideways as to present his largest view, bending his head and tail toward the intruder, and as a last resort, striking with his head. During courtship, a male elassomatid displays toward a female by bobbing up and down and waving his fins, while swimming toward the spawning site. When a female approaches, the male develops a bright spawning coloration and begins to tremble, while bumping and nipping at the female. Courtship continues for several minutes before the release of eggs and milt.

Feeding ecology and diet

Many centrarchids and percids are near or at the top of the food chain in their habitats. Largemouth bass and walleye, for example, are typically top predators, feeding on herbivorous as well as smaller carnivorous fishes. Even the much smaller yellow perch and bluegill are primarily carnivorous and will take invertebrates and minnows. Centrarchids also include a number of specialized mollusk-feeding forms, such as the longear and the red-ear (*Lepomis microlophus*) sunfishes. Many centrarchids and percid species are known as crepuscular feeders, but anglers often take considerable numbers of

School of yellow perch (*Perca flavescens*). (Illustration by Emily Damstra)

The rainbow darter (*Etheostoma caeruleum*) has been found in almost every state of the United States east of the Mississippi River and west of the Appalachian Mountains. (Photo by Animals Animals ©Raymond A. Mendez. Reproduced by permission.)

these species at midday (although fishing does peak around dawn and dusk).

Some centrarchids are also known to alter their feeding ecology depending on the species composition of their neighbors. Bluegills living in waters with predatory largemouth basses, for instance, are more likely to forage in weeds rather than in open water. This action may protect them from the jaws of a bass, but it also limits their ability to find food. Additional studies of bluegill and pumpkinseed sunfishes report that they will shift their diet to zooplankton or bottom-dwelling prey in deference to the apparently dominant green sunfish (*L. cyanellus*) when all three occur together. Elassomatids and moronids are also carnivorous. Both eat invertebrates, especially crustaceans, and adult moronids are also piscivorous.

Predation on the species within these four families is primarily by larger piscivorous fishes. For example, northern pike (*Esox lucius*) will eat even quite large yellow perch, which will, in turn, feed on smaller fishes. Other predators of shallow water fishes include piscivorous birds, such as herons and ospreys.

Reproductive biology

Percid reproduction varies. Some scatter their eggs and milt into the water or over vegetation, while others spawn over gravel nests. Some species deposit individual eggs; others, such as the yellow perch and the European perch (*Perca fluviatilis*), lay their eggs in masses. Some species, such as the yellow perch and sauger (*Stizostedion canadense*), leave the area almost immediately after spawning; others, such as the johnny darter and tessellated darter (*Etheostoma olmstedi*), remain with their eggs until hatching. Among centrarchids, the bluegill and longear sunfishes prefer to spawn in still waters, others, including many darters, opt for the running water of a stream.

During mating season, males generally develop brighter coloration, which apparently assists in attracting females and announcing their territories to other males. Sunfishes spawn in one of three ways. A male may make a nest and attract females for mating there. Females may spawn with smaller males known as satellite and sneaker males. During breeding season, satellite males take on coloration of a female and trick the nesting male into allowing them to approach, giving them access to females coming to the nest. Sneaker males hide among vegetation near a nesting male's site, watch the females arrive, then dash through the nest site ejecting milt as they reach the females. Non-nesting males mature earlier than nesting males, commonly going through the sneaker stage when they reach the age of two years, then becoming satellite males in later years. Nesting males are usually older individuals that top the seven-year mark. Some controversy exists over whether elassomatids are nest builders. Scientists have reported spawning with and without nests in some species, leading to the hypothesis that substrate conditions determine whether nesting occurs.

Of the moronids, perhaps most is known about the behavior of the striped sea bass, probably because of its popularity as a sport fish. These fishes inhabit coastal waters along both the Atlantic (its native distribution) and Pacific coasts. The Pacific introduction can be traced to 1879 and 1882, when the fishes were translocated to the San Francisco shore. Striped sea basses are migratory, moving to cooler northern waters in summer and warmer southern waters in the fall. As breeding season approaches, they return to their home stream to spawn, apparently via olfactory cues. Feeding ceases prior to the annual breeding season, during which the fishes engage in broadcast spawning. One study of the European sea bass (*Dicentrarchus labrax*) indicated that its gender can be influenced by temperature. Experiments showed that temperature differences during the development of eggs could affect the ultimate sex ratio.

Bluegills (*Lepomis macrochirus*) occur in all three drainage basins in Wisconsin (Lake Michigan, Mississippi River, and Lake Superior). (Photo by Animals Animals ©E. R. Degginger. Rerpoduced by permission.

Conservation status

Careful monitoring of species fished for sport maintains these populations in adequate numbers. Nongame species, and those with very small distributions, fare less well. For example, numerous darter species, which are neither sport fishes nor broadly distributed, are listed as threatened or endangered. Some species in these families have been widely introduced outside of their geographic ranges. The successful naturalization of percids and centrarchids in areas well outside of their aboriginal ranges has often had deleterious effects upon faunas of indigenous fishes.

The IUCN Red List categorizes 1 species from this group as Extinct; 2 species as Critically Endangered; 4 species as Endangered; 30 species as Vulnerable; 12 species as Lower Risk/Near Threatened; and 7 as Data Deficient.

Significance to humans

A great number of species within these four families are prized sport fishes. Examples are walleye and perch in the family Percidae, as well as both large- and smallmouth bass in the family Centrarchidae. A few, such as the banded pygmy sunfish (*Elassoma zonatum*) are considered indicator species, and provide scientists with information about the environmental health of a particular waterway. Several members of these families, particularly the yellow perch and walleye (in the family Percidae), are commercial food fishes.

1. Logperch (*Percina caprodes*); 2. Breeding male rainbow darter (*Etheostoma caeruleum*); 3. Ruffe (*Gymnocephalus cernuus*); 4. Blue-spotted sunfish (*Enneacanthus gloriosus*); 5. Rock bass (*Ambloplites rupestris*); 6. Female black crappie (*Pomoxis nigromaculatus*). (Illustration by Emily Damstra)

1. Banded pygmy sunfish (*Elassoma zonatum*); 2. Male yellow perch (*Perca flavescens*); 3. Walleye (*Stizostedion vitreum*); 4. Largemouth bass (*Micropterus salmoides*); 5. Male longear sunfish (*Lepomis megalotis*); 6. Bluegill (*Lepomis macrochirus*); 7. Striped sea bass (*Morone saxatilis*). (Illustration by Emily Damstra)

Species accounts

Rock bass
Ambloplites rupestris

FAMILY
Centrarchidae

TAXONOMY
Ambloplites rupestris Rafinesque, 1817, Lakes of New York, Vermont, United States. No subspecies are recognized.

OTHER COMMON NAMES
English: Goggle eye, northern rock bass, redeye; French: Crapet de roche; German: Gemeiner felsenbarsch, gemeiner sonnenbarsch.

PHYSICAL CHARACTERISTICS
Maximum total length 17 in (43.2 cm), typically little more than one-half that. Large-mouthed, red-eyed fish with rows of small, chocolate-colored squares along the sides of its greenish to brownish body.

DISTRIBUTION
North America from the Mississippi Valley almost to the Atlantic coast, and Lake Winnipeg to Missouri and the northern boundaries of Georgia and Alabama. Also widely introduced worldwide.

HABITAT
Heavily vegetated areas of freshwater lakes and ponds, as well as clear, rocky streams.

BEHAVIOR
Schools in winter, becomes solitary when breeding season commences in the spring.

FEEDING ECOLOGY AND DIET
Feeds on aquatic plants, invertebrates, and fishes, occasionally conspecifics.

REPRODUCTIVE BIOLOGY
Spawns in late spring and early summer over male-constructed and guarded nests. The demersal, adhesive eggs hatch in three to four days. The male continues to protect the young as long as they remain in the nest area. Once they scatter, usually within a few days, protection ceases. They reach sexual maturity at three to five years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Minor sport and commercial fishes. ◆

Blue-spotted sunfish
Enneacanthus gloriosus

FAMILY
Centrarchidae

TAXONOMY
Enneacanthus gloriosus Holbrook, 1855, South Carolina, Georgia, and Cooper Rivers, South Carolina, United States. No subspecies are recognized.

OTHER COMMON NAMES
German: Kiemenfleck-diamantbarsch.

PHYSICAL CHARACTERISTICS
Maximum total length 3.7 in (9.5 cm). Similar in general appearance to a bluegill, but with proportionally longer fins; dark "teardrop" band beneath eye; vertical, dark banding on body; and numerous metallic blue spots in the head, body, and vertical fins.

DISTRIBUTION
Eastern United States, from southern New York to western Florida.

HABITAT
Prefers vegetated freshwater lakes, ponds, pools, and stream backwaters.

BEHAVIOR
Solitary; seldom strays far from cover. Easily dominated by other centrarchids; typically found in substantial numbers only in habitats *Lepomis* species do not find congenial, such as the highly acidic black waters of the New Jersey pine barrens.

FEEDING ECOLOGY AND DIET
Normally feeds on snails and other invertebrates near cover of vegetation.

REPRODUCTIVE BIOLOGY
Males build nests 4–12 in (10.2–30.5 cm) in diameter in algae or soft substrate. Spawning occurs in spring, perhaps extending from late winter to early summer. Little is known of its reproductive biology in the wild.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sometimes kept as an aquarium fish. ◆

Bluegill
Lepomis macrochirus

FAMILY
Centrarchidae

TAXONOMY
Lepomis macrochirus Rafinesque, 1819, Ohio River, United States. Two or three subspecies are recognized.

OTHER COMMON NAMES
English: Bluegill sunfish, sunfish; German: Blauer Sonnenbarsch; Spanish: Pez sol.

PHYSICAL CHARACTERISTICS
Maximum total length 16 in (41 cm). Broad, rather flat fish with a small mouth. Distinguished from its relatives by an all-black opercular flap, general gray-blue coloration, a dark spot at the rear edge of the soft dorsal fin, and dark banding on the sides of the body.

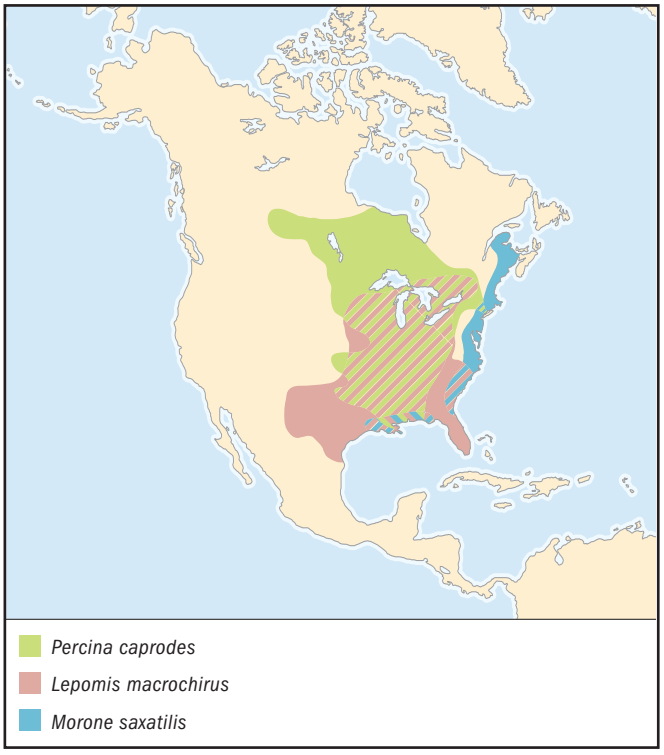
DISTRIBUTION
Common in North America from southern Canada to northern Mexico; widely introduced throughout the world.

HABITAT
Freshwater, inland waters from large lakes to small ponds, also slow-moving streams. Prefers some type of cover, such as rocky or vegetated areas.

BEHAVIOR
Schooling fishes. Schools of several dozen smaller fishes ranging up to 4 in (10.2 cm) long are commonly seen along lake shores in 1–2 ft (0.3–0.6 m) of water, darting from beneath docks and boats. Larger fishes generally remain further from shore in deeper water. Cleaning behavior has been recorded for Florida populations.

FEEDING ECOLOGY AND DIET
Mainly diurnal feeders. Diet comprises invertebrates and small fishes.

REPRODUCTIVE BIOLOGY
Breeds in the late spring and early summer, when groups of males enter shallow water to begin building nests, which are depressions in the substrate. The male guards its nest. Females may also spawn with smaller males known as satellite and sneaker males, which take on the female coloration and fool nesting males into allowing them to approach and mate with females coming to the nest. Sneaker males may also lie in ambush in vegetation near a nesting male's site, wait for females to arrive, then quickly swim through the nest site, ejecting milt. The spherical, demersal eggs, which are laid singly or in small clusters, typically hatch in two to three days. Bluegills in the field typically attain sexual maturity at two to three years and about 4–5 in (10.2–12.7 cm) in length. Bluegills hybridize with pumpkinseeds and many other sunfish species.



CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sport and minor commercial food and aquarium fishes. ◆

Longear sunfish
Lepomis megalotis

FAMILY
Centrarchidae

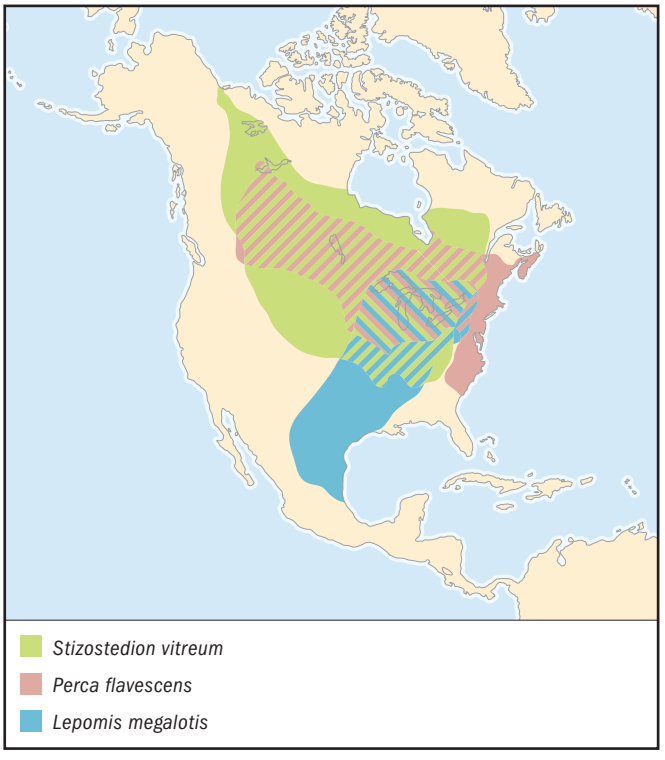
TAXONOMY
Lepomis megalotis Rafinesque, 1820, Licking and Sandy Rivers, Kentucky, United States. Five or six subspecies are recognized.

OTHER COMMON NAMES
English: Creek perch, Great Lakes longear, northern longear.

PHYSICAL CHARACTERISTICS
Maximum total length 9.5 in (24 cm). Similar in body shape to bluegill, but with a notably larger opercular flap, especially in the adult male. Young olive with yellow specks; adults red above and orange below, and decorated on the body with small, blue spots and on the opercle with blue, curving lines.

DISTRIBUTION
Northeast North America, from northeastern Mexico and north to the Great Lakes.

HABITAT
Prefers shallow, weedy waters of lakes and ponds; also found in quiet streams.



BEHAVIOR
During the spring-to-summer breeding season, males prepare nests in shallow waters along the shoreline. More than one females may approach one male's nest. Spawning occurs over the nests, and the male offers parental care to the young. In addition, some males engage in the sneaker-spawning behavior typical of many centrarchids.

FEEDING ECOLOGY AND DIET
Feeds in shallow waters on small mollusks, insects, and small fishes. Predators include other piscivorous fishes.

REPRODUCTIVE BIOLOGY
Females lay demersal, adhesive eggs, which hatch in three to seven days. Sexual maturity occurs at about two to three years.

CONSERVATION STATUS
American and Canadian populations are not considered to be at risk. Mexican populations are threatened by degradation of their habitat due to poor water-management practices.

SIGNIFICANCE TO HUMANS
The basis for a recreational fishery; sometimes kept as an aquarium fish. ◆

Largemouth bass
Micropterus salmoides

FAMILY
Centrarchidae

TAXONOMY
Micropterus salmoides Lacepède, 1802, Carolinas, United States. Two subspecies are recognized.

OTHER COMMON NAMES
English: Green bass, largemouth black bass, northern largemouth bass; French: Achiganà grande bouche; German: Forellenbarsch; Spanish: Huro, lobina negra.

PHYSICAL CHARACTERISTICS
Maximum total length 38 in (97 cm). About one-third as wide as long, distinguished in part by a deeply cut dorsal fin. Differs from its relative the smallmouth bass (*M. dolomieui*) by its lack of horizontal striping on the head, the presence of a dark horizontal stripe on each side of the body instead of vertical banding, and a maxillary that reaches just past the eye.

DISTRIBUTION
North America from the Great Lakes east to the Atlantic coast, and from Lake Winnipeg south to northern Mexico. Also widely introduced throughout the United States and around the world, including Europe, South America, and Africa.

HABITAT
Freshwater fish, prefers lakes, ponds, swamps, and river/stream backwaters with considerable hiding places, including thick vegetation or rocky structures.

BEHAVIOR
Juveniles school, but adults are solitary animals that remain near cover, such as logs or heavy vegetation and seldom venture into waters deeper than 20 ft (6 m).

FEEDING ECOLOGY AND DIET
Diurnal feeder on crustaceans and other invertebrates, also fishes.

REPRODUCTIVE BIOLOGY
Spawns in the late spring and early summer. The male becomes territorial and makes depressions in the substrate of weedy areas to serve as nests. A single female may lay eggs over several nests. Both males and females provide parental care, and have been known to guard the eggs and young for up to a month after hatching. Parental care continues as long as the young fishes remain schooled.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Part of a large, popular fishing industry in the United States and Canada. ◆

Black crappie
Pomoxis nigromaculatus

FAMILY
Centrarchidae

TAXONOMY
Pomoxis nigromaculatus Lesueur, 1829, Wabash River, Indiana, United States. No subspecies are recognized.

OTHER COMMON NAMES
English: Calico bass, grass bass, moonfish, oswego bass, speckled bass, strawberry bass; French: Marigane noire.

PHYSICAL CHARACTERISTICS
Maximum total length 19.3 in (49 cm). Rather flat, broad, silvery fishes with sloping foreheads and a black, mottled pattern on the sides. Fins are also noticeably mottled. The similar white crappie (*P. annularis*) is less mottled and has vertical banding on its sides.

DISTRIBUTION
Central and eastern North America, south to Florida and Texas, United States, and north to Quebec and Manitoba, Canada. Widely introduced throughout the United States and other countries.

HABITAT
Freshwater species. Prefers clear, weedy lakes, ponds, and slow-stream backwaters.

BEHAVIOR
Schools during the day in deep water around structures. Crepuscular feeder; moves to shallower water to feed. Exciting sport fish that puts up a good fight when hooked by anglers.

FEEDING ECOLOGY AND DIET
Feeds both amidst vegetation and in open waters on small fishes and invertebrates. Primarily feeds at dawn and dusk.

REPRODUCTIVE BIOLOGY
Spawning occurs in late spring and early summer. Males make nests, sometimes near other males, in the substrate of weedy or rocky areas. Females may mate with several males. Females lay spherical, demersal, adhesive eggs singly or perhaps in small clumps. Males guard the eggs and young, which hatch in two to three days. Reach sexual maturity by two to four years old.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Fished for sport in the United States and Canada. ◆

Banded pygmy sunfish
Elassoma zonatum

FAMILY
Elassomatidae

TAXONOMY
Elassoma zonatum Jordan, 1877, Little Red River, Arkansas; R. Brazos, Texas; United States. No subspecies are recognized.

OTHER COMMON NAMES
German: Gebänderter Zwergbarsch.

PHYSICAL CHARACTERISTICS
Maximum total length 1.9 in (4.8 cm). White and grayish black, speckled fish with two stripes on the anterior sides of the body. One stripe extends from the mouth through the eye, and the other begins above and behind the eye. Tail and fins are also speckled.

DISTRIBUTION
South-central United States south of a line from southern Illinois to North Carolina.

HABITAT
Muddy-bottomed freshwaters, including swamps and other weedy aquatic areas.

BEHAVIOR
Normally solitary; males in limited space will defend their territories against encroachment by other males. Territorial displays include a more intense body coloration, a rapid beating

of the tail and pectoral fins, and if necessary, a quick strike at the intruder.

FEEDING ECOLOGY AND DIET
Carnivore; feeds on crustaceans, worms, and other invertebrates.

REPRODUCTIVE BIOLOGY
During breeding season, the male takes on brighter coloration and begins enticing a female to his spawning site by wiggling all his fins in a distinctive pattern. Once a female appears receptive, the male trembles and "points" to the site with his snout, and then gently prods the female. Nest building may or may not occur, perhaps depending on the suitability of the substrate. Relatively little is known of its reproductive biology in the wild.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Of minor importance to the pet trade, also important as indicator species of environmental quality. ◆

Striped sea bass
Morone saxatilis

FAMILY
Moronidae

TAXONOMY
Morone saxatilis Walbaum, 1792, New York, United States. No subspecies are recognized.

OTHER COMMON NAMES
English: Linesider, roccus, rock, rockfish, striped bass, striper bass; French: Bar d'Amérique, bar rayé; Spanish: Lubina estriada.

PHYSICAL CHARACTERISTICS
Maximum total length 6.6 ft (2 m). Body silver, with more or less interrupted, black, parallel stripes along the sides of the body.

DISTRIBUTION
Tributaries along the U.S. Atlantic coast, also Gulf of Mexico west to Louisiana; widely introduced throughout the United States and other countries.

HABITAT
Fresh and brackish bays and tributaries, also inland coastal waterways. Found in rivers during spawning.

BEHAVIOR
Social; typically lives in large size-graded schools. When handled or threatened, responds with grunts and clicks as it attempts an escape.

FEEDING ECOLOGY AND DIET
Carnivores; larvae feed on zooplankton, juveniles eat various invertebrates, and adults take invertebrates and fishes.

REPRODUCTIVE BIOLOGY
Broadcast spawners, produce fairly buoyant eggs during an annual reproductive season. Eggs are laid in moving water, which keeps the eggs afloat until they hatch in two to seven days. No parental care for eggs or young. Males reach maturity at about two to three years and 12–15 in (30.5–38 cm); females at about three to four years and 20–24 in (51–61 cm) long.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Important sport and minor commercial food fishes. ◆

Rainbow darter
Etheostoma caeruleum

FAMILY
Percidae

TAXONOMY
Etheostoma caeruleum Storer, 1845, Fox River, Illinois, United States. No subspecies are recognized.

OTHER COMMON NAMES
German: Regenbogen-Springbarsch.

PHYSICAL CHARACTERISTICS
Maximum total length 3 in (7.7 cm). Brownish orange fish with about a dozen vertical, green bands on the sides of its body and green markings on its face. It has two dorsal fins.

DISTRIBUTION
Eastern North America from southern Ontario, Canada to Mississippi and Louisiana, and from Minnesota to West Virginia in the United States.

HABITAT
Bottom-dwelling, freshwater fishes that inhabit the swift currents of creeks, as well as average-to-small rivers.

BEHAVIOR
Solitary, stations in the lee of rocks as it moves over the bottom in search of food. Individuals are very wary and seek shelter among rocks at the slightest disturbance.

FEEDING ECOLOGY AND DIET
Feeds primarily on crustaceans and invertebrates, but also eats fish eggs and larvae. Feeding can involve suction, in which they draw water and prey into their mouths, or diving head-first toward sandy and gravely substrate after prey.

REPRODUCTIVE BIOLOGY
Males become more brightly colored during breeding season, which occurs in the spring. Females wait in slower waters of a stream, half-buried in the substrate, while males enter stream riffles. As a female approaches the spawning site, a male swims up, following her closely and defending her from any other interested males. He continues to maintain this "moving territory" until mating occurs. During mating, males align themselves next to the female and spawn while both vibrate. Females typically lay three to seven eggs at a time, but spawn multiple times, sometimes laying up to 1,000 eggs per season. Females typically bury their eggs, which hatch in 10–12 days. They reach sexual maturity at one year.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Ruffe
Gymnocephalus cernuus

FAMILY
Percidae

TAXONOMY
Gymnocephalus cernuus Linnaeus, 1758, European lakes. No subspecies are recognized.

OTHER COMMON NAMES
English: Pope; French: Frash, grémille; German: Kaulbarsch, Pfaffenlaus; Spanish: Acerina.

PHYSICAL CHARACTERISTICS
Maximum total length 9.8 in (25 cm). Small, dark-spotted, brownish fish with 15 to 19 long dorsal spines. Dorsal fins are fused.

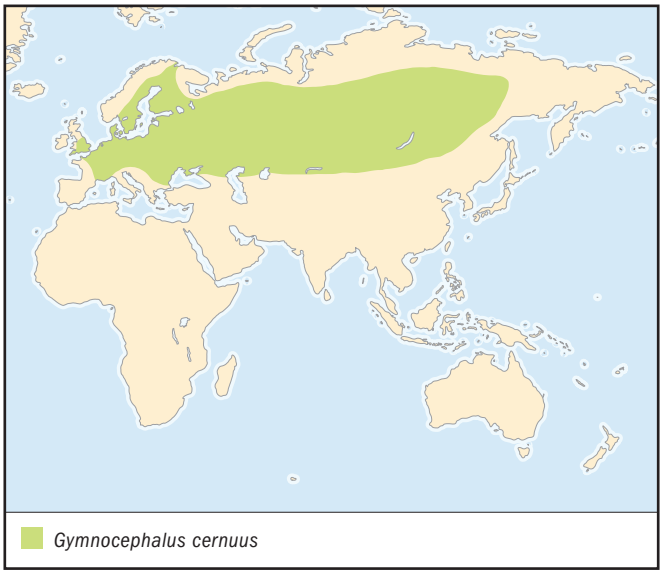
DISTRIBUTION
France to eastern Siberia. Accidentally introduced to Lakes Superior and Michigan in the United States.

HABITAT
Prefers deep waters of lakes and ponds, but also found in streams.

BEHAVIOR
Releases alarm pheromones that alert conspecifics to danger. Adults have particularly well-developed neuromasts, sensory organs that can detect even slight vibrations in the water and thus allow the fishes to hunt for food in the cover of darkness.

FEEDING ECOLOGY AND DIET
Nocturnal feeders of shallow-water zooplankton.

REPRODUCTIVE BIOLOGY
Spawns in shallow water, where strands of sticky, whitish yellow, demersal eggs adhere to weeds and/or rocks along the bottom. No parental care for eggs or young, which hatch in 5–12 days. They attain sexual maturity in two to three years at 4.3–4.7 in (11–12 cm) in length. In warmer areas, sometimes become sexually mature in just one year.



CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sport and minor food fishes. Considered an undesirable, invasive species in the Great Lakes, where it likely arrived via ballast water from Eurasian ships. ◆

Yellow perch
Perca flavescens

FAMILY
Percidae

TAXONOMY
Perca flavescens Mitchill, 1814, New York, United States. No subspecies are recognized.

OTHER COMMON NAMES
English: American perch, lake perch, perch; French: Perchaude, perche canadienne, perche jaune; German: Amerikanischer Flußbarsch.

PHYSICAL CHARACTERISTICS
Maximum total length 19.7 in (50 cm), but anglers rarely see one longer than 12 in (30.5 cm). Greenish yellow, full-bodied, fusiform fishes with six to nine vertical dark bars along the sides.

DISTRIBUTION
North America from northwestern Canada to the far northwestern United States, through central and southern Canada, the north-central United States, and the Great Lakes region, and into the southeastern Canadian provinces, as well as the eastern United States south to South Carolina. Also introduced to various locations around the world. In North America, for instance, it has been introduced to the western and southern United States and has spread into British Columbia in western Canada.

HABITAT
Freshwater streams, rivers, ponds, and lakes. Prefers sites with submerged vegetation, also inhabits brackish water and salt lakes.

BEHAVIOR
Shoals of young fishes are commonly seen in very shallow waters near shore, often darting between docks in water less than 3 ft (0.9 m) deep. Shoals of larger fishes prefer somewhat deeper waters.

FEEDING ECOLOGY AND DIET
Feeds on small to large insects and other invertebrates, fish eggs, and fishes, sometimes taking bait almost as large as themselves. Predators include larger fishes, walleye, smallmouth bass, northern pike (*Esox lucius*), and numerous salmon species.

REPRODUCTIVE BIOLOGY
Spawns from late winter to midsummer. They frequently lay their long, spiral egg masses in vegetation. There is no parental care.

CONSERVATION STATUS
Not threatened, although stocks in many areas have been severely overexploited, and these fisheries are increasingly regulated by fishery managers.

SIGNIFICANCE TO HUMANS
Commercial food and sport fishes. ◆

Logperch
Percina caprodes

FAMILY
Percidae

TAXONOMY
Percina caprodes Rafinesque, 1818, Ohio River, United States. Three subspecies are recognized.

OTHER COMMON NAMES
English: Manitou darter, zebrafish; French: Dard-perche, fouille-roche.

PHYSICAL CHARACTERISTICS
Maximum total length 7 in (18 cm). Long, fusiform fishes with conical nose and banding on the sides of the body that becomes more irregular posteriorly. Body color is greenish brown.

DISTRIBUTION
North America from Hudson Bay east to the Atlantic coast, west to Saskatchewan, and south through the Great Lakes region to the Gulf of Mexico.

HABITAT
Spread through many habitats, but primarily gravel- or sandy-bottomed, medium-sized rivers. Also bottom dweller in weedy lakes, usually some distance from the shoreline.

BEHAVIOR
Perhaps their most notable behavior occurs during feeding, when they frequently use their noses to root prey out of the substrate and from beneath stones.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, particularly copepods.

REPRODUCTIVE BIOLOGY
Moves into shallow waters or rivers to spawn in the spring. The male becomes more vividly colored and develops tubercles on its ventral side. A gravid female approaches a school of males, which follows her to the substrate. Following the release of eggs and milt, the female and often the males engage in rapid wriggling, which serves to churn up the bottom and bury the eggs. No parental care for eggs or young.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Walleye
Stizostedion vitreum

FAMILY
Percidae

TAXONOMY
Stizostedion vitreum Mitchill, 1818, Cayuga Lake, Ithaca, New York, United States. Two subspecies are recognized.

OTHER COMMON NAMES
English: Walleyed pike, blue pike, gray pike, green pike, yellow pike, pickerel, dory, glass eye, marble eye, pikeperch; French: Doré doré jaune; German: Amerikanischer Zander.

PHYSICAL CHARACTERISTICS
Maximum total length 42 in (107 cm), but fishes below (often well below) 24 in (61 cm) are the norm. Long, fusiform body with large, translucent eyes. Body is typically brownish.

DISTRIBUTION
Most of the United States and Canada, except for far northern and eastern Canada, and far southern and western United States.

HABITAT
Freshwater (rarely brackish); inhabits lakes, ponds, and larger rivers, prefers sites with shallow, somewhat murky waters.

BEHAVIOR
Beginning in late winter, small groups of up to a half-dozen males will begin chasing one or two gravid females. The females are noticeably larger than the pursuing males. Eventually, the females will lead the groups to very shallow water, sometimes only a few inches below the surface, for a single night of spawning.

FEEDING ECOLOGY AND DIET
Feeding sessions begin at sunset and carry on into the night. An opportunistic predator, the diet comprises fishes, especially yellow perch and invertebrates, but it is also known to take frogs and mudpuppies.

REPRODUCTIVE BIOLOGY
A broadcast spawner, reproduces over a variety of substrates, including sandy, gravelly, or rocky lake and river bottoms, as well as stream vegetation, usually in an area where the water is moving either via a slow current or shoreline waves. The female scatters her eggs. Breeding occurs in spring to early summer, sometimes even in late winter. Egg production in the females begins much earlier, and anglers find females well laden with eggs in early winter. Eggs hatch in one to two weeks. No parental care of eggs or young.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Major sport fishes and minor commercial food fishes. ◆

Resources

Books

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Nelson, Joseph S. *Fishes of the World.* New York: John Wiley & Sons, Inc., 1994.

Periodicals

Jones, W. J., and J. M. Quattro. "Phylogenetic Affinities of Pygmy Sunfishes (*Elassoma*) Inferred from Mitochondrial DNA Sequences." *Copeia* 199, no. 2 (1999): 470–474.

Koumoundouros, G., M. Pavlidis, L. Anezaki, C. Kokkari, A. Sterioti, P. Divanach, and M. Kentouri. "Temperature Sex Determination in the European Sea Bass, *Dicentrarchus labrax* (L., 1758) (Teleostei, Perciformes, Moronidae): Critical Sensitive Ontogenetic Phase." *Journal of Experimental Zoology* 292, no. 6 (2002): 573–579.

Maniak, P. J., R. D. Lossing, and P. W. Sorensen. "Injured Eurasian Ruffe, *Gymnocephalus cernuus*, Release an Alarm Pheromone that Could Be Used to Control Their Dispersal." *Journal of Great Lakes Research* 26, no. 2 (2000): 183–195.

Organizations

American Fisheries Society. 5410 Grosvenor Lane, Suite 110, Bethesda, MD 20814-2199 USA. Phone: (301) 897-8616. Fax: (301) 897-8096. E-mail: main@fisheries.org Web site: <http://www.fisheries.org/>

North American Native Fishes Association. 1107 Argonne Dr., Baltimore, MD 21218 USA. Phone: (410) 243-9050. E-mail: nanfa@att.net Web site: <http://www.nanfa.org>

Other

"Animal Diversity Web." University of Michigan Museum of Zoology [cited January 20, 2003]. <http://animaldiversity.ummz.umich.edu>

Finley, L. "An Introduction to *Enneacanthus obesus* (Girard), the Banded Sunfish (with Special Reference to Rhode Island Distribution)." The North American Native Fishes Association [cited January 20, 2003]. <http://www.nanfa.org/articles/acobesus.htm>

"TNHC: The North America Freshwater Fishes Index" [cited January 20, 2003]. <http://www.tmm.utexas.edu/tnhc/fish/na/naindex.html>

Leslie Ann Mertz, PhD

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Percoidei II

(Bluefishes, dolphinfishes, roosterfishes, and remoras)

Class Actinopterygii
Order Perciformes
Suborder Percoidei
Number of families 4

Photo: A leaping dolphinfish (*Coryphaena hippurus*) near Baja California. Dolphinfish are also known as mahi-mahi and dorado. (Photo by Lawrence Naylor/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The suborder Percoidei contains more than 70 families and 2,800 species. This chapter focuses on the families Pomatomidae, Coryphaenidae, Nematistiidae, and Echeneidae. The bluefish (Pomatomidae) and the dolphinfishes (Coryphaenidae) are two small families of streamlined pelagic fishes. The bluefish is monotypic and dates from the Miocene epoch. The dolphinfishes consist of just one genus, *Coryphaena*, and two species. These fishes likely date from the Eocene and sometimes are grouped together with the Nematistiidae (roosterfish), Echeneidae (remoras), Rachycentridae (cobia), and Carangidae (jacks and trevallys). The roosterfish, *Nematistius pectoralis*, is a monotypic species within its family. Remoras consist of four genera and eight species. The genera are *Echeneis* (two species), *Phtheirichthys* (one species), *Remora* (four species), and *Remorina* (one species).

Physical characteristics

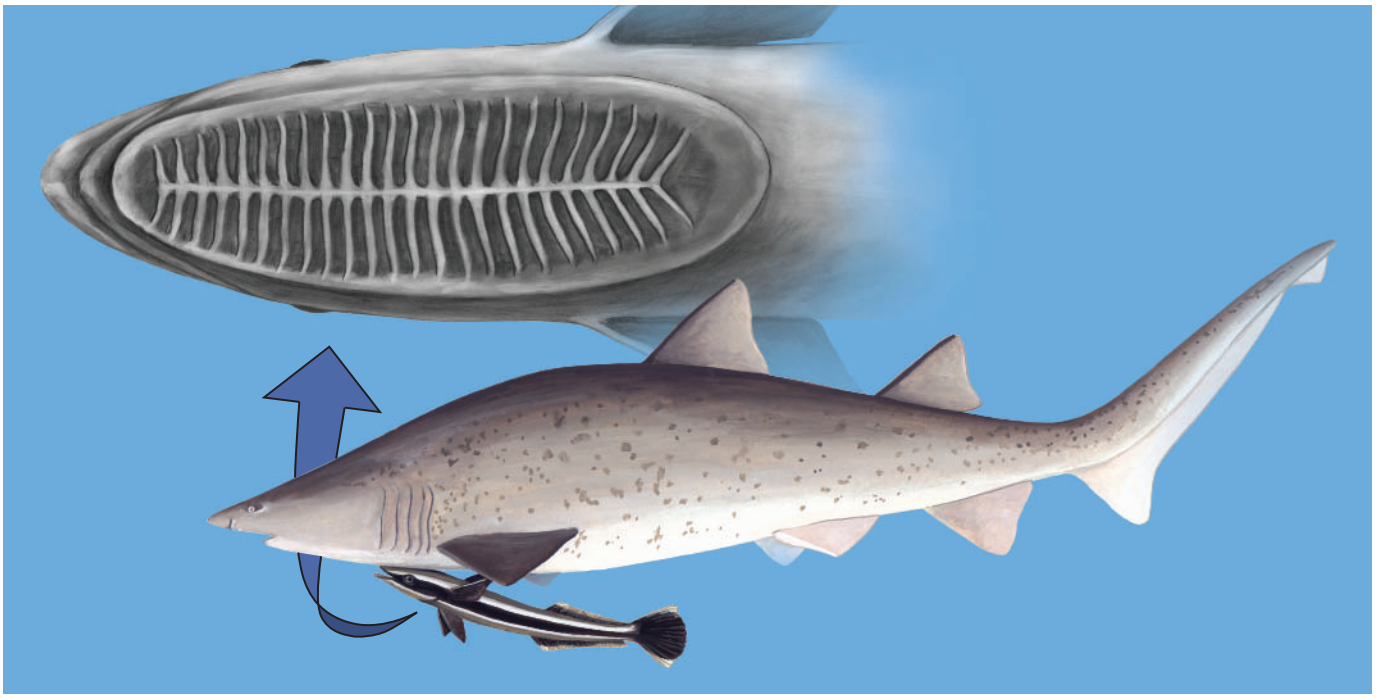
Percoids have elongated, fusiform bodies with forked or slightly forked caudal fins. Bluefishes have two dorsal fins, a long anal fin, and a mouth well armed with sharp, compressed teeth arrayed in a single series. They grow to about 51 in (130 cm) in length. Adult male dolphinfishes have pronounced bony crests on the heads; these fishes also have long, continuous dorsal and anal fins and brilliant yellow, green, and blue coloration. They grow to about 83 in (210 cm) in length. The roosterfish has an elongated, fusiform body with a raised head profile dorsally and a dorsal fin containing seven remarkably long spines. The remoras are streamlined, elongated, or club-shaped, with a flattened head that has a sucking disc modified from a dorsal spine. The disc has between 10 and 28 movable lamina that allow it to grasp the body surface of a host. The dorsal fin is positioned just ahead of the caudal peduncle and has 18–40 soft rays. The anal fin also has 18–40 soft rays. The scales are cycloid and small, and the swim bladder is absent. Remoras have a highly modified dorsal surface on the head that acts as a suction disc. This disc allows remoras to attach themselves to the body surfaces of various hosts. Body coloration ranges from black to combinations of blue, black and white. Body sizes range from 20 to over 44 in (50 to over 110 cm). Remoras are remarkably adapted for a commensal relationship with numerous host organisms and clean their hosts in exchange for "hitching rides" and feeding on leftover food items. The bluefish, the dolphinfishes, and the roosterfish have evolved to become efficient predators in open waters or inshore habitats.

Distribution

The bluefish ranges widely across three oceans and is found in marine and brackish waters of the eastern and western Atlantic Ocean, the Mediterranean Sea, the Black Sea, the Indian Ocean, and the southwest Pacific Ocean; it is absent from the eastern and northwestern Pacific and almost all of the central Pacific. The dolphinfishes occur in tropical and warm temperate marine waters of the Atlantic, Indian, and Pacific Oceans. The roosterfish is distributed in the eastern Pacific from southern California south to Baja California, Mexico, the Galapagos Islands, and Peru. The remoras occur in tropical and warm temperate waters of the Atlantic, Indian, and Pacific Oceans.

Habitat

The bluefish is pelagic but generally is found inshore off headlands and beaches and enters brackish water habitats, such as estuaries, to forage. Dolphinfishes are pelagic in surface



Modified dorsal fin of the remora, which allows it to stick to large fish and take a "free ride." (Illustration by Emily Damstra)

waters but also move inshore to forage, usually at insular localities where deep water is close to shore. The roosterfish prefers inshore areas, particularly sandy beaches; this species also frequents the water column away from beaches. Juveniles appear in tide pools. The remoras utilize their hosts as a microhabitat, whether swimming in surface waters of the pelagic realm or in inshore habitats.

Behavior

Bluefishes form schools or loose aggregations that are effective in hunting prey. These schools migrate seasonally, moving predictably to warm water during the cool or winter season and to cooler water during the warm or summer season. Dolphinfishes form schools that migrate over large distances on a seasonal basis. Small groups hover under floating objects, such as tree trunks or fish aggregation devices, and schools also follow boats and ships. The roosterfish may be solitary and usually swims inshore along sandy beaches as it forages for food. Remoras utilize their specialized sucking discs to attach themselves to sharks, skates, rays, billfishes, and other large fishes as well as sea turtles, dolphins, and whales. Occasionally, they are seen swimming freely. The attachment behavior allows them to function as transportation parasites, in that their host species do most of the swimming while the remora goes along for the ride, moving only to change position along the host's body, when feeding or moving between hosts, or when reproducing.

Feeding ecology and diet

Bluefishes, dolphinfishes, and roosterfishes are predators. Bluefishes are voracious predators of fishes, squids, and other shoaling animals and continue to attack prey even after satiation. Dolphinfishes feed upon small fishes, squids, and other pelagic prey. The roosterfish feeds on smaller fishes and other pelagic prey inshore or just offshore. In contrast, remoras feed on external parasites, mainly copepods, of host organisms but also take leftover items not consumed by their predatory hosts.

Reproductive biology

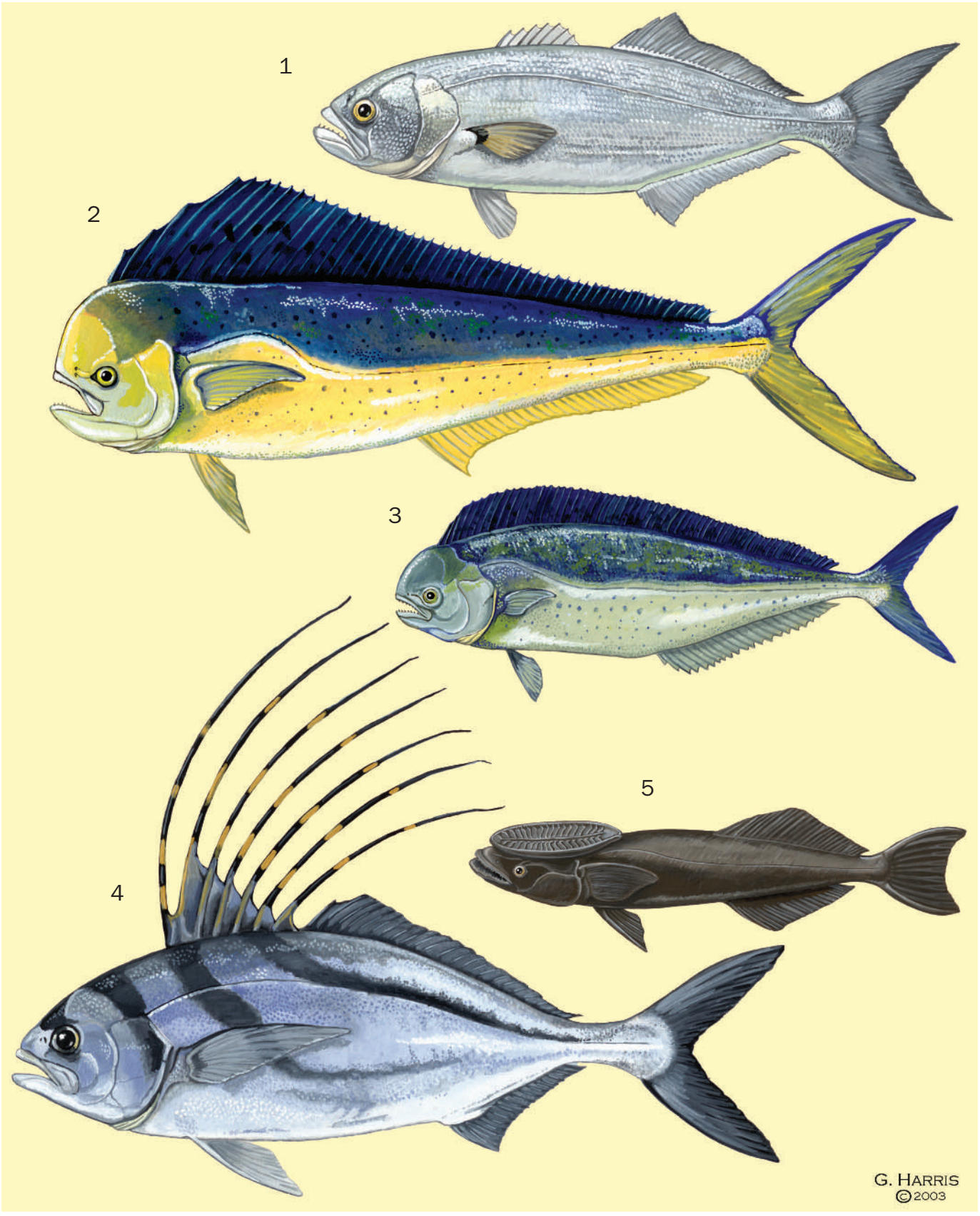
Bluefishes court and spawn in schools or groups, spawn seasonally, and produce pelagic eggs and larvae. Dolphinfishes court and spawn in schools or groups and produce pelagic eggs and larvae. One species has been spawned in captivity. The reproductive biology of roosterfishes apparently is not well known. They are likely pelagic spawners, perhaps in groups, and they produce pelagic eggs and larvae. Little is known about the reproductive biology of remoras. They presumably pair-spawn. Eggs and larvae probably are pelagic.

Conservation status

None of these fishes is listed by the IUCN, but they are subject to overfishing, either commercial or sport, or are caught as by catch.

Significance to humans

The bluefish and the dolphinfishes are very important commercial, recreational, and subsistence fishes. Both the bluefish and the common dolphinfish have been raised by aquaculture. The roosterfish is an important game fish that also is taken in subsistence and artisanal fisheries. Remoras may be taken incidentally for display in public aquaria.



1. Bluefish (*Pomatomus saltatrix*); 2. Common dolphinfish (*Coryphaena hippurus*); 3. Pompano dolphinfish (*Corphaena equiselis*); 4. Roosterfish (*Nematistius pectoralis*); 5. Common remora (*Remora remora*). (Illustration by Gillian Harris)

Species accounts

Pompano dolphinfish
Coryphaena equiselis

FAMILY
Coryphaenidae

TAXONOMY
Coryphaena equiselis Linnaeus, 1758, type locality not specified.

OTHER COMMON NAMES
English: Pompano dolphin; Japanese: Ebisu-shiira.

PHYSICAL CHARACTERISTICS
Body is fusiform and elongate, with a vertical head profile and a bony crest in adults, especially males; it is much less pronounced than in the common dolphinfish. The single dorsal fin has 52–59 soft rays and extends from just behind the gills down to the caudal peduncle. The anal fin is long, with 24–28 soft rays, and extends from the anus to the caudal peduncle. The caudal fin is forked. Body color is metallic blue and green on the back and silver with gold spots and a golden sheen on the flank, with a dark dorsal fin. Upon death, the dorsal color fades to gray. The caudal fin margin of juveniles is white. Grows to 50 in (127 cm) in length but lives only 4 years.

DISTRIBUTION
Tropical and some subtropical seas worldwide.

HABITAT
Pelagic but ventures inshore to forage off reefs or emergent rocks.

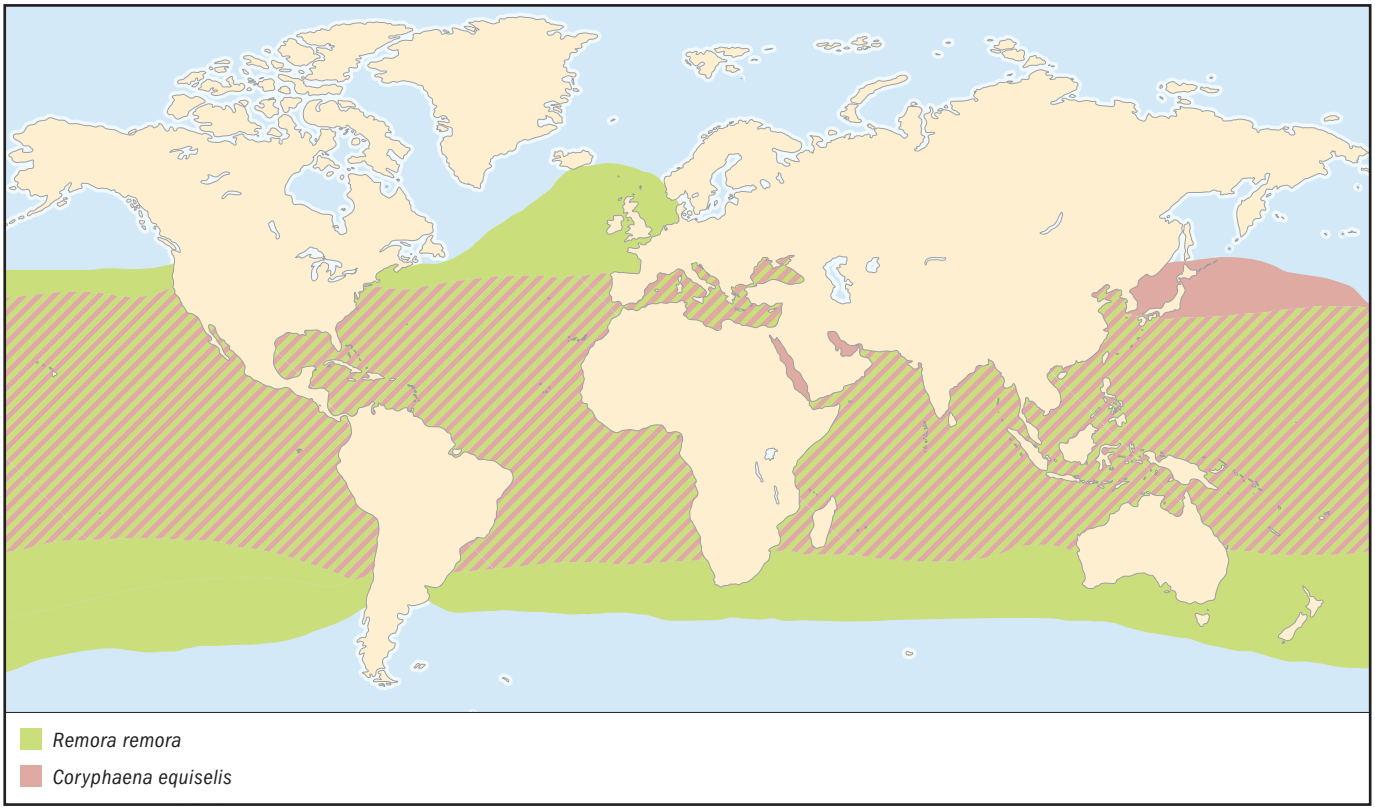
BEHAVIOR
A schooling species that swims in pelagic surface waters but also ventures inshore. Follows boats or hovers under floating structures, such as tree trunks or palm leaves. Attracted to fish aggregation devices.

FEEDING ECOLOGY AND DIET
Preys on smaller fishes and squids in addition to miscellaneous pelagic prey, which it hunts in schools or groups.

REPRODUCTIVE BIOLOGY
Reproduction is not well known, but apparently it courts and spawns in groups or aggregations and produces pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN, but may be vulnerable to overfishing. Recognized under Annex I of the 1982 Convention on the Law of the Sea because of its migratory habits.

SIGNIFICANCE TO HUMANS
A minor commercial species sought after by consumers for its excellent food quality. It is highly prized in sport fisheries, especially off South America. Also taken in subsistence fisheries. ◆



Common dolphinfish
Coryphaena hippurus

FAMILY
Coryphaenidae

TAXONOMY
Coryphaena hippurus Linnaeus, 1758, type locality not specified.

OTHER COMMON NAMES
English: Dolphin, dorado, mahi-mahi; Spanish: Dorado; Hawaiian: Mahi-mahi; Japanese: shiira.

PHYSICAL CHARACTERISTICS
Elongate and fusiform body. A long dorsal fin, with 58–66 soft rays, arises above the eye and extends to the caudal peduncle. The anal fin is concave, has 25–31 soft rays, and extends from the anus to the caudal peduncle. The pectoral fin is more than half the length of the head, and the caudal fin is forked. Adult males have a pronounced bony crest on the front of the head. Brilliantly colored, with metallic greens and blues on the back and flanks, gold on the flanks, and yellow and white shades on the venter. Juveniles and young adults have vertical bars on the flanks. Grows to longer than 83 in (210 cm) but lives for only about 5 years.

DISTRIBUTION
Tropical, subtropical, and warm temperate waters worldwide.

HABITAT
Inhabits pelagic surface waters but ventures inshore to forage. Reported to enter brackish waters, such as estuaries.

BEHAVIOR
Forms highly migratory schools, aggregations, or groups. Attracted to boats, ships, and floating objects, such as palm fronds or tree trunks. Also attracted to fish aggregation devices.

FEEDING ECOLOGY AND DIET
A predator upon smaller fishes and squids but also takes pelagic crustaceans and even macroplankton.

REPRODUCTIVE BIOLOGY
This species matures sexually in the wild at only 4–5 months. Females mature at about 13.5 in (34.3 cm) and males at 16.5 in (42 cm) fork length (the distance between the snout and the midpoint in the "fork" of the caudal fin). Eggs are pelagic, buoyant, spherical, about 0.05 in (1.4 mm) in diameter, and clear in color; the oil globule is yellow. Eggs hatch after 1.5 days and larvae measure just under 0.16 in (4 mm) at hatching. Melanophores develop on the head, trunk, and tail soon afterwards. Larvae begin to feed upon planktonic copepods after the yolk sac is absorbed, and growth is rapid.

CONSERVATION STATUS
Not listed by the IUCN, but may be vulnerable to overfishing. Recognized under Annex I of the 1982 Convention on the Law of the Sea because of its migratory habits.

SIGNIFICANCE TO HUMANS
A highly prized commercial and game fish that also is taken in subsistence fisheries. Reported to be ciguatoxic in some areas. Ciguatera poisoning is caused by the cumulative deposition of a class of polyether toxins within the tissues of fishes. The toxins are produced by certain microscopic dinoflagellate organisms of the genus *Gambierdiscus*, and are transmitted by the mechanism of the food chain, increasing in intensity by a factor

of ten in each successive level within the chain. The common dolphinfish acquires these toxins from prey fishes, which in turn acquire them from smaller fishes or zooplankton that have ingested dinoflagellate during feeding. If this fish is consumed by man, the concentrated poison contained within its tissues causes neurological damage that may be fatal. ◆

Common remora

Remora remora

FAMILY
Echeneidae

TAXONOMY
Remora remora Linnaeus, 1758, Indian Ocean.

OTHER COMMON NAMES
Japanese: Nagakoban.

PHYSICAL CHARACTERISTICS
Body is elongate, robust, and clublike, with a large, flat head and a large sucker disc. Dorsal and anal fins are positioned just forward of the caudal peduncle. There are 22–26 soft rays in the dorsal fin and 22–24 soft rays in the anal fin. The caudal fin is large and somewhat truncated. The coloring is a dark, brownish gray. Reaches nearly 35 in (90 cm) in length and just over 2.2 lb (1 kg) in weight.

DISTRIBUTION
Circumglobal in tropical, subtropical, and warm temperate waters of the Pacific, Atlantic, and Indian Oceans. Also found in the Mediterranean. Reported from Iceland and Scandinavia, presumably during warmer months.

HABITAT
Attaches to host organisms, such as sharks, rays, seaturtles, billfishes, other large fishes, and even ships. Pelagic but also appears inshore.

BEHAVIOR
Attaches itself to host organisms and hitches rides. Swims freely, on occasion. Otherwise, behavior is not well known.

FEEDING ECOLOGY AND DIET
Feeds on parasitic copepods attached to host organisms. Also takes leftover scraps from the host's feeding events.

REPRODUCTIVE BIOLOGY
Not well known. Likely pair-spawns pelagic eggs and has pelagic larvae. Spawning may be seasonal, especially at higher latitudes.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
May be taken incidentally for public aquaria or as bycatch from shark fisheries. ◆

Roosterfish

Nematistius pectoralis

FAMILY
Nematistiidae

TAXONOMY
Nematistius pectoralis Gill, 1862, Cape Saint Lucas, Baja California, Mexico.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body fusiform and elongate, with a raised profile of the head that extends to the dorsal fin. The first dorsal fin has seven long spines that retract into a groove; it may have a signal function, or it may be used in maneuvering when attacking prey. A second dorsal fin has 25–28 soft rays. There are three spines and 15–17 soft rays in the anal fin. The caudal fin is forked. Body color is blue dorsally and silvery white ventrally. There are black stripes positioned obliquely on the dorsal surface; one runs up onto the upper lobe of the caudal fin. Grows to nearly 65 in (165 cm) in length, with a weight of nearly 115 lb (52 kg).

DISTRIBUTION
Eastern Pacific from southern California, where it is rare, south through Baja California, Mexico, and the Gulf of California, where it is more common, and down to Peru and west to the Galápagos Islands.

HABITAT
Mainly inshore or near-coastal habitats, especially off sandy beaches.

BEHAVIOR
Not well known. Usually solitary or travels in small groups.

FEEDING ECOLOGY AND DIET
A predator upon fishes and other smaller pelagic organisms.

REPRODUCTIVE BIOLOGY
Reproduction not well known. Likely a pelagic spawner, with pelagic eggs and larvae. May spawn in groups. Spawning probably is seasonal, especially at higher latitudes.

CONSERVATION STATUS
Not listed by the IUCN, but vulnerable to overfishing.

SIGNIFICANCE TO HUMANS
An important game fish that also is taken as a commercial and subsistence food fish. Some collected incidentally for public aquaria. ◆

Bluefish

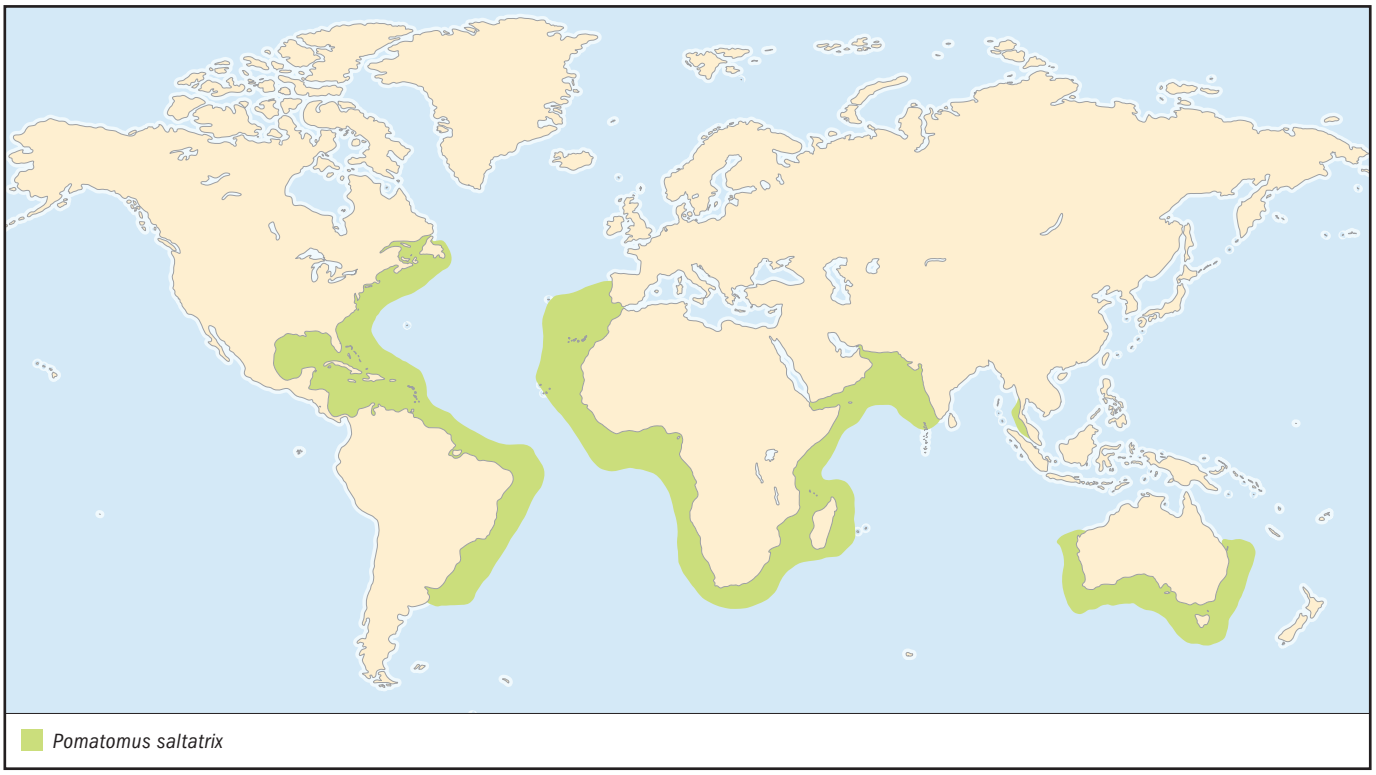
Pomatomus saltatrix

FAMILY
Pomatomidae

TAXONOMY
Pomatomus saltatrix Linnaeus, 1766, Carolina, United States.

OTHER COMMON NAMES
English (Australia): Tailor.

PHYSICAL CHARACTERISTICS
Body fusiform and elongate, with two dorsal fins, an elongate anal fin, and a slightly forked caudal fin. There are seven to eight spines in the first dorsal fin and one spine and 13–28 soft rays in the second dorsal fin. The anal fin has two to three spines and 12–27 soft rays. Both the dorsal and anal fin soft rays have a scaly appearance. There is a black blotch at the base of each of the pectoral fins. The mouth has sharp and



compressed jaw teeth arranged in a single prominent series. The preopercle has a membranous flap that extends over the subopercle. Color is silvery blue or greenish blue on the back, with silvery flanks and belly. Grows to 51 in (130 cm) length and lives as long as nine years.

DISTRIBUTION
Favors subtropical waters but enters tropical and temperate waters seasonally. In the eastern Atlantic it occurs from Portugal south to South Africa, including Madeira and the Canary Islands; it also may be found in the Mediterranean and Black Seas. In the western Atlantic, it is distributed from Canada to Florida and Bermuda and south as far as Argentina. In the Pacific, it is found throughout most of Australia, except for the Northern Territory but is absent from the northwest Pacific, virtually all of the central Pacific, and the eastern Pacific. In the Indian Ocean, this species ranges from East Africa and Madagascar north to southern Oman and east to southwest India, the Malay Peninsula, and Western Australia. Records from Hawaii and Taiwan require verification, and those from New Guinea, Indonesia, and the Northern Territory of Australia probably are in error.

HABITAT
Pelagic but prefers inshore waters and often is found off rocky or sandy headlands, beaches, and breakwaters. Enters estuaries. Moves with the tide.

BEHAVIOR
Adults form schools or loose aggregations. Individuals are reported to move in association with sharks and billfishes. Juveniles form schools. Schools migrate seasonally.

FEEDING ECOLOGY AND DIET
Highly predatory. Schools or aggregations forage inshore and in open water, attacking schools of prey, mainly smaller fishes and squids, and continues to attack after having fed to satiation. Dangerous if handled, because it bites out of water and reportedly has severed fingers or caused serious wounds. Is reported to attack splashing swimmers, too.

REPRODUCTIVE BIOLOGY
Spawning is seasonal, usually in spring and summer months (May–August in the northwest Atlantic; March–May and September–November in the southwest Atlantic, north of the equator; September–December in the Southern Hemisphere), and occurs serially. Females are remarkably fecund, with egg counts ranging from 400,000–2,000,000 depending upon body size of the female. Eggs are pelagic and buoyant, about 0.04 in (1.09 mm) in diameter, and hatch after 1.5–2 days. Larvae are pelagic, possess large heads and mouths, and acquire teeth on both jaws by the time they reach 0.13 in (3.3 mm) in length. The yolk sac disappears soon afterwards and larvae become predacious. Dorsal, anal, and caudal fins differentiate at about 0.25 in (6.35 mm), and fin rays appear at about 0.33 in (8.4 mm). Dorsal spines develop more fully at 1.1 in (27.9 mm). Pigmentation is apparent on the head dorsally and on the gut at 0.33 in (8.4 mm), with very small dots appearing on the entire body at 1.1 in (27.9 mm).

CONSERVATION STATUS
Not listed by the IUCN, but vulnerable to overfishing on both commercial and recreational scales. Has been caught for sport but is wasted because the flesh degrades quickly without proper handling. Population sizes are cyclical.

SIGNIFICANCE TO HUMANS
Very important commercial species that also is a significant and prized game fish. ◆

Resources

Books

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767.
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Terry J. Donaldson, PhD

Percoidei III

(Grunters, temperate basses and perches, snooks and giant perches, and relatives)

Class Actinopterygii
Order Perciformes
Suborder Percoidei
Number of families 7

Photo: A common snook (*centropomus undecimalis*) swimming in the Florida Keys, USA. (Photo by Larry Lipsky. Bruce Coleman, Inc. Reproduced by permission.)

Evolution and systematics

The suborder Percoidei contains more than 70 families and 2,800 species. This chapter focuses on the following seven families: the grunters or tigerfishes (Terapontidae: 15 genera; 48 subspecies), the temperate basses and austral perches (Percichthyidae: 11 genera; 31 subspecies), the blackfishes (Gadopsidae: 1 genus; 2 subspecies), the pygmy perches (Nannopercidae: 3 genera; 6 subspecies), the Chilean perches (Percilidae: 1 genus; 2 subspecies), the kuhlias or flagtails (Kuhliidae: 2 genera; 10 subspecies), and the snooks and giant perches (Centropomidae: 4 genera; 23 subspecies). The Percichthyidae is a loosely organized family in need of revision. Previous authors have placed the Gadopsidae, Nannopercidae, and Percilidae within this family. These fishes are recognized in this chapter as separate from the percichthyids because of disparate fin counts or their unique patterns of endemism. The blackfishes and pygmy perches are endemic to Australia, while the Chilean perches are endemic to Chile in South America. This separation has been recognized in Allen et al. (2002), and in part in Froese and Pauly (2002). The families Percichthyidae, Gadopsidae, Nannopercidae, and Percilidae, all likely date from the Eocene period. The Centropomidae date from the Cretaceous period. Freshwater grunters date back to the late Cretaceous or early Tertiary periods. Allen et al. (2002) reported that a fossil terapontid unearthed in Queensland, Australia, was dated from the Oligocene, thus indicating that grunters had been present in Australia 30 million years ago. The history of the Kuhliidae is uncertain, but the family likely dates from the Eocene.

Physical characteristics

The fishes grouped in this chapter are typically bass or perchlike in their morphology and appearance. Grunters have bodies that are oblong and compressed slightly, a sloping head with an operculum bearing two spines, and conical or flattened teeth on the jaws. Some species have enlarged "blubber lips" as adults. The dorsal fin is notched with 11–13 spines and 9–11 soft rays. There are 3 spines on the anal fin and 7–10 soft rays. The pelvic fins have 1 spine and 5 soft rays, and are positioned just behind the base of the pectoral fins. The caudal fin may be emarginate, truncate, or rounded. Grunters derive their common name from their ability to contract muscles adjacent to the swim bladder (which acts as an amplifier) to produce gruntlike sounds when alarmed, stressed, or removed from the water. They may reach at least 31.5 in (80 cm) in total length. The temperate basses and austral perches include some of the largest of freshwater fishes, and certainly among the largest perciform fishes. Many have elongate bodies and large mouths, although some have a pronounced hump or steeply sloping head. The dorsal fin is single and notched, and the anterior pelvic fin rays are elongate. Their lateral line is continuous and complete, and their scales are small, primarily ctenoid, but cycloid to a lesser extent.

Percichthyids may reach up to 71 in (180 cm) total length. Blackfishes have slender, elongate bodies; a somewhat blunt snout; a long single dorsal fin; and a somewhat long anal fin. The pelvic fins are jugular xand consist of just a single branched ray. The caudal fin is rounded. The lateral line is reasonably well developed and the scales are minute. Black-

fishes may grow up to 23.6 in (60 cm) total length. Pygmy perches have small, slender bodies; small mouths; interrupted lateral lines that are poorly developed or even absent; and a notched dorsal fin. These fishes are all less than 3.9 in (10 cm) total length, and usually much shorter. Chilean perches are also small, usually less than 3.9 in (10 cm) total length, and have slender, perchlike bodies with truncate or slightly emarginate caudal fins.

Kuhlias are usually oval shaped and compressed, have large eyes relative to the size of their heads, and have a silver or grayish color. The caudal fin is forked or nearly so and often distinctly marked. The dorsal fin has 10 spines, 9–12 soft rays, and is deeply notched. The anal fin has 3 spines and 9–12 soft rays. The opercle has 2 spines, and the pelvic fins lack an axillary process. The lateral line is well developed.

Snooks and giant perches have large, elongate, perchlike bodies. The snout may be concave. Most species are silvery in color. The lateral line is continuous and extends from just behind the gill well onto the caudal fin. The caudal fin may be forked, truncate, or rounded. The dorsal fin is either deeply notched or has a pronounced gap between the first part (7–8 spines) and second part (1 spine and 8–11 soft rays). The anal fin has 3 spines and 6–9 soft rays, and the pelvic fin has 1 spine and 5 soft rays. Males and females are sexually dimorphic for body size, with females being larger. Adults range in size from 7.9 in to over 78.7 in (20–200 cm) total length. The Nile perch is the largest and grows to at least 441 lb (200 kg).

Distribution

The Terapontidae occurs in freshwater, brackish, and coastal marine waters of the Indo-Pacific. A number of them, including *Amniataba* (one species), *Bidyanus* (two subspecies), *Hannia* (one species), *Hephaestus* (13 subspecies), *Pelates* (three subspecies), *Pelsartia* (one species), *Pingalla* (one species), *Scortum* (three subspecies), *Syncomistes* (four subspecies), and *Varichthys* (two subspecies), have limited or endemic freshwater and brackish-water (some also marine) distributions in Australia and New Guinea. Others, such as *Pelates* and *Terapon* (three subspecies), are widely distributed from East Africa east to Southeast Asia, Japan, Australia, New Caledonia, and Lord Howe Island, or more narrowly in the western Pacific (for example, the monotypic *Rhynchopelates oxyrhynchus*). The genus *Mesopristes* has one species endemic to Madagascar and another to Fiji, in addition to two that occur more widely in the western Pacific. The genus *Leiopotherapon* has one species endemic to Luzon Island, Philippines, and another two that are endemic to Australia, whereas *Lagusia micracanthus* is endemic to Sulawesi, Indonesia. *Pelates quadrilineatus*, a wide-ranging Indo-West Pacific species, has also colonized the eastern Mediterranean from the Red Sea by way of the Suez Canal.

The Percichthyidae occurs in tropical, subtropical, and temperate marine and fresh waters of the Atlantic, Indian, and Pacific Oceans. A number have limited or endemic distributions in the fresh or brackish waters of Australia and include *Bostockia* (one species), *Guyu* (one species), *Maccullochella* (three subspecies, but one with two subspecies), and *Macquaria* (four subspecies). *Percichthys* (five subspecies) is endemic to freshwaters in Argentina and Chile. *Coreoperca*, (three subspecies), *Coreosiniperca* (one species) and *Sinoperca* (five subspecies) are endemic to freshwaters of China, Korea, and Japan. The genus *Lateolabrax* has two species limited to coastal, brackish, or fresh waters of Japan. *Bathysphyraenops simplex* is widely distributed in coastal waters of the Indo-Pacific and Atlantic regions. The four species of the genus *Howella* are bathypelagic in the open ocean. The closely related Gadopsidae (genus *Gadopsis*, two subspecies) and Nannopercidae (genus *Edelia*, one species; genus *Nannatherina*, one species; and genus *Nannoperca*, four subspecies) are endemic to Australia. The Percilidae (genus *Percilia*; two subspecies) are endemic to Chile in South America.

The Kuhliidae are distinguished by wide-ranging Indo-Pacific species (including *Kuhlia mugil*, *K. marginata*, and *K. rupestris*), but there are also a number of limited-distribution or endemic species. *Kuhlia caudavittata* is limited to fresh and brackish waters of Reunion, Mauritius, Rodriguez, and Madagascar in the Indian Ocean. The Pacific Ocean counterpart is *K. boninensis*, which occurs in the Ogasawara and Ryukyu Islands of Japan, but is also found at larger islands in Micronesia and also at Tahiti. Three species endemic to their localities in the Pacific region include *K. munda* from fresh and brackish waters in New Caledonia, *K. nutabunda*, a marine species from Easter Island, and *K. sandivicensis* from marine, brackish, and fresh waters of the Hawaiian Islands. A monotypic genus, *Parakuhlia*, has been reported from the Atlantic.

The family Centropomidae includes 12 species of snooks (*Centropomus* spp.) found in warm marine and brackish waters of the western Atlantic and eastern Pacific, from the southern United States south to Brazil in the Atlantic, and Baja California and the Gulf of California south to Peru in the Pacific. *Hypoterus macropterus* is endemic to Western Australia in coastal waters of the southeast Indian Ocean. Six species of *Lates* are endemic to the Rift Lakes of East Africa (Lakes Albert, Rudolf, Tanganyika, and Turkana) and a seventh, the notorious Nile perch (*L. niloticus*) is present in some Rift Lakes, but also many of the major river systems of Africa and brackish water lakes of Egypt. This species was introduced into Lake Victoria with highly disastrous effects upon the endemic and greatly diverse fish fauna. Two other species of *Lates* are distributed in marine, brackish, and fresh waters of the Indo-West Pacific. The Japanese giant perch (*L. japonica*) is found in coastal waters and streams of Japan. The highly prized barramundi (*L. calcarifer*) occurs in Australia and New Guinea, but can also be found from the Arabian Gulf east to China and southern Japan, and south through Indonesia. Another Indo-West Pacific species is *Psammoperca waigiensis*, which ranges in marine and brackish waters from the Bay of Bengal in the Indian Ocean east to Southeast Asia, China, Japan, the Philippines, and Indonesia, and south to northern Australia.

Habitat

Members of this group are found in marine, brackish, and fresh waters. Among the grunters, *Amniataba* occur in ponds, lakes, and reservoirs, as well as fast-flowing streams or pools in those streams; one species also ventures into mangroves in

estuaries. *Bidyanus* and *Syncomistes* also occur in rivers, lakes, or reservoirs. Inhabitants of fast or occasionally slow-flowing rivers or rocky creeks include *Hannia*, *Hephaestus*, *Leiopotherapon*, and *Pingalla*. One species of *Leiopotherapon* has adapted to high-salinity desert waters. *Scortum* subspecies prefer clear streams or rivers, but are also found in lakes. Inhabitants of slow-flowing, turbid rivers and streams, or swamps include *Pingalla*. Lake-dwelling grunters include *Hephaestus*. *Lagusia*, *Mesopristes*, *Pelates*, *Pelsartia*, *Rhynchopelates*, and *Terapon* can be found in fresh and brackish water reaches of rivers and streams, or in bays.

Percichthyids are found mainly in freshwater streams, rivers, or lakes. A few species occur in reservoirs. Some species, such as *Lateolabrax*, also enter estuaries and are found in coastal waters. However, *Howella* spp. are an exception. They are pelagic in mid- or deepwater depths and migrate towards the surface at night. Some species may be benthic as adults. The blackfishes are found mainly in clear rivers or streams, sometimes at higher elevations. Pygmy perches prefer either streams and rivers, ponds, or wetlands. The Chilean perches are also found in streams.

Kuhlias inhabit coastal marine and brackish waters, usually in the water column. Some species have adapted to freshwater habitats, mainly rivers and streams, and one, *K. rupestris*, is well adapted to upper freshwater reaches. Juveniles of marine species frequent tide pools. The snooks and giant perches are either resident in marine or estuarine waters, usually in association with mangroves or lower freshwater reaches of rivers (i.e., *Centropomus*, *Hypopterus*, *Lates*, and *Psammoperca*) or freshwater lakes, reservoirs, and rivers (such as *Lates*). Adults of some species may frequent deeper water than juveniles.

Behavior

The grunters are quite variable in their general behavior. Some species are solitary and frequently associate with structures such as rocks, logs, flooded trees, or emergent vegetation. Others form large schools, often up in the water column and over deep water, or hugging the bottom in shallower water. The temperate basses and austral perches are often solitary or occur in small groups, usually in association with structure. At least one species is segregated by sex; female Australian basses (*Macquaria novemaculeata*) move to the upper reaches of streams, whereas males move downstream. Some species, such as the nightfishes, are nocturnal. *Howella* move up and down in the water column in relation to night and day. The blackfishes hug the bottom, patrol home ranges, and are active at night. Pygmy perches are often solitary and swim in midwater where they forage for prey or lurk near shelter, such as emergent vegetation. Little is known about the behavior of Chilean perches, but it is presumed that they associate with structure or the bottom. Kuhlias usually aggregate in schools and move in and out of surge zones. Species in freshwater streams often associate with structure or aggregate, as juveniles and young adults, in pools. Snooks and giant perches are often solitary, but may also occur in small groups. Many undertake seasonal migrations into estuaries, usually in relation to patterns of freshwater runoff, but some marine species also migrate into freshwater.

Barramundis (*Lates calcarifer*) are important commercial fish. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Grunters prey upon fishes, insects, and benthic invertebrates, including crustaceans, worms, and mollusks, but some are also omnivorous or herbivorous and will feed upon benthic algae, plant roots, palm berries, or other plant life. Members of the genus *Syncomistes* have mouths modified for scraping algae off rock surfaces. Adult percichthyids are largely carnivores, although juveniles may feed upon zooplankton. Freshwater species feed upon insects, mollusks, crustaceans, fishes, fish eggs and fry, or amphibians. Some larger species will also take reptiles, birds, and even aquatic mammals. Marine and estuarine species also feed upon fishes and crustaceans; deep-dwelling species feed upon macroplankton, crustaceans, and fishes in the water column. Blackfishes feed upon a wide range of items, including worms, insects, crustaceans, small fishes, and even fish eggs. Pygmy perches feed on terrestrial and aquatic insects (including their larvae) and microcrustaceans. Chilean perches likely also feed upon insects, crustaceans, and small fishes. Kuhlias feed upon small crustaceans and fishes, but those living in freshwater may also feed upon insects and even fruits, such as figs, that fall into the water. Snooks and giant perches are predatory fishes that feed mainly upon other fishes and crustaceans; juveniles in freshwater will also feed upon insects. They are skillful at ambushing prey. Members of the families featured in this chapter may be preyed upon by larger predator fishes and birds, and in some cases by marine and aquatic reptiles and mammals.

Reproductive biology

Mating strategies, courtship, spawning, and postspawning investment by parents is variable within this group. Freshwater grunters migrate upstream or into the shallows of lakes to spawn, usually during summer months (wet season), although occasionally between autumn and late winter (dry season). Migrations are usually triggered by changes in water temperature, rising water levels in response to seasonal rains, or both. Spawning takes place during daylight or night, may be in groups, and results in the release of eggs that fall onto the substrate. Eggs hatch within 36 hours, and the larvae develop relatively rapidly and disperse soon after. Marine species spawn in the sea and the juveniles migrate into fresh or brackish water.

The diversity of this group dictates that the reproductive biology of these fishes is variable. Age of maturity will vary both between species and within species. An example of variation within species is the nightfish *Bostockia porosa*. Males of this species mature after their first year, but females are not mature until their second year. Generally, freshwater percichthyids spawn during the spring and summer months, and fishes often migrate upstream or downstream to spawning sites. Many of these traditional sites have been obstructed by dams or other barriers to migration, and this has resulted in corresponding declines in population sizes of various species. Reproductive effort may be considerable in these fishes. Members of the genus *Coreoperca* have male parental care of eggs and larvae. The trout cod (*Maccullochella macquariensis*) spawns demersal eggs that are large and adhesive onto hard surfaces such as rocks. Parental care is practiced by males of this and other species in this genus. In rivers, care extends until flooding occurs; flooding makes food items, such as insect larvae, available to the postlarval fishes. In the golden perch (*Macquaria ambigua*), eggs are floating and no care is practiced. Others of this genus scatter eggs that are either pelagic or that sink into interstices within the substrate, and are not cared for. The reproductive biology of other freshwater species is not that well known. Among marine species, members of the genus *Howella* likely breed in aggregations and scatter pelagic eggs into the water column. *Lateolabrax* spp. spawn during winter and scatter eggs on deeper rocky reefs of coastal waters. Juveniles may migrate upriver after recruiting from the ocean. The blackfishes mature in two to three years and practice pair spawning during summer months. Females enter a male's nest and lay eggs, usually one batch that varies in number from 20–500, depending upon the species and her size, and these and the subsequent larvae are guarded by the male until they disperse. Pygmy perches are mature in about one year. Depending upon the species, spawning begins late in the austral winter (dry season) and continues through early summer (wet season). Males are territorial, assume bright colors, defend nest sites, and attract females to spawn. Females spawn multiple small batches of eggs every few days during a period that can last for several weeks. The eggs are spawned upon aquatic algae or the substrate within a male's territory. The eggs hatch within two to four days. Most adults of at least one species, *Nannatherina balstoni*, die after spawning. The reproductive biology of the Percilidae is not well known. Presumably, spawning also occurs sometime between the austral spring and summer. Eggs are likely demersal and may be guarded by the male.

Kuhlias in freshwater are catadromous, which means that they migrate downstream to spawn in estuaries or the open ocean. Marine species also spawn in the ocean. Tropical species may spawn all year long but seasonal peaks may occur. Spawning behavior is not well known. The spawning mode is pelagic, with spawning in groups. The eggs and larvae are pelagic; larvae of freshwater species migrate into freshwater streams and rivers.

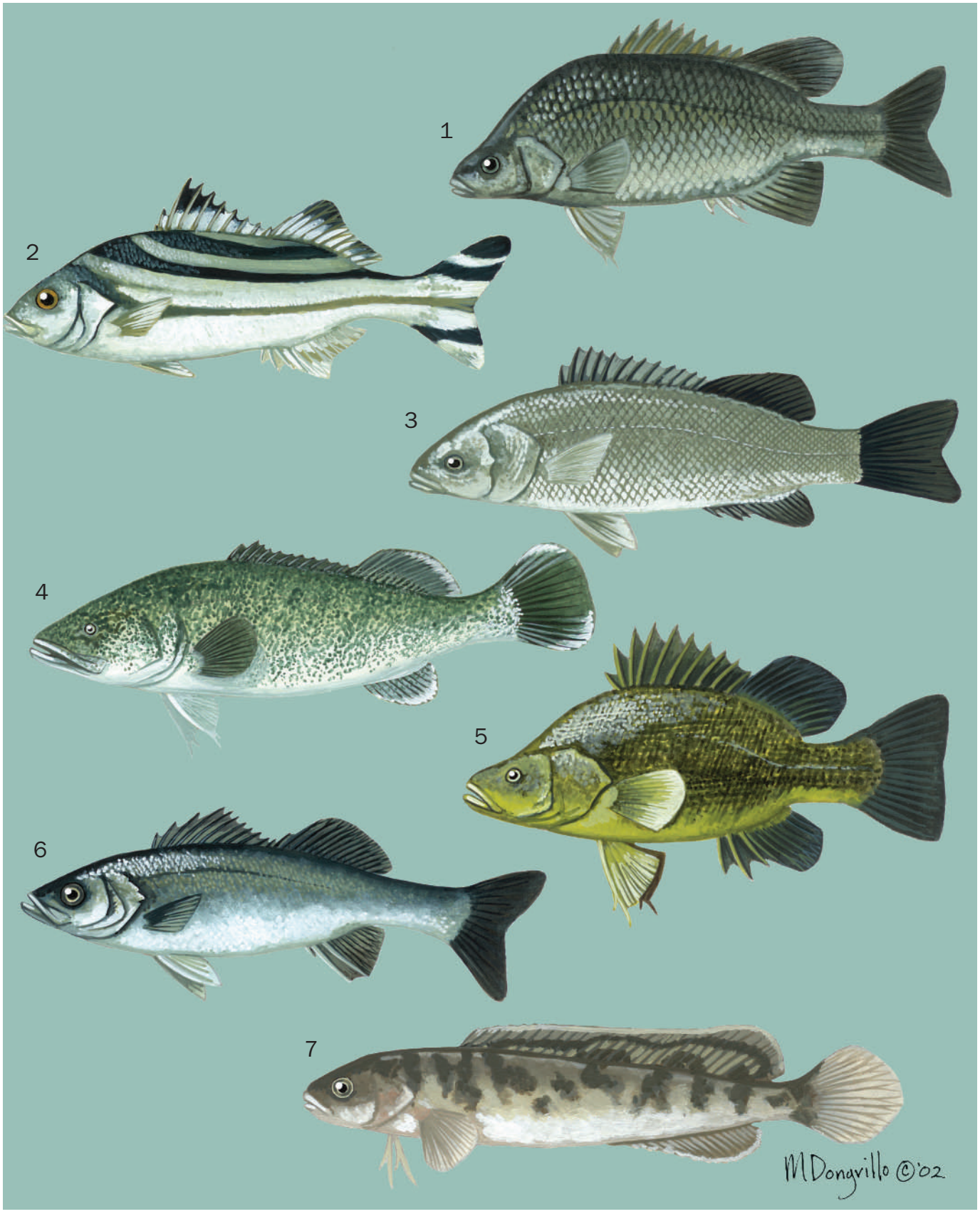
Marine and brackish water centropomids form spawning aggregations in estuaries or reef passes. *Lates* spp. are catadromous and spawn in groups or pairs (not always within groups) in estuaries and nearshore waters. Females are generally larger than males, and two or more males have been observed courting much larger females. Eggs and larvae are pelagic. The reproductive behavior of African lake species of this genus is not well known, but courtship and spawning in groups or pairs, usually after migration to a specific site, with the release of pelagic eggs, is likely. Both *Hypoterus macropterus* and *Psammoperca waigiensis* probably migrate to estuaries or inshore waters to spawn pelagic eggs.

Conservation status

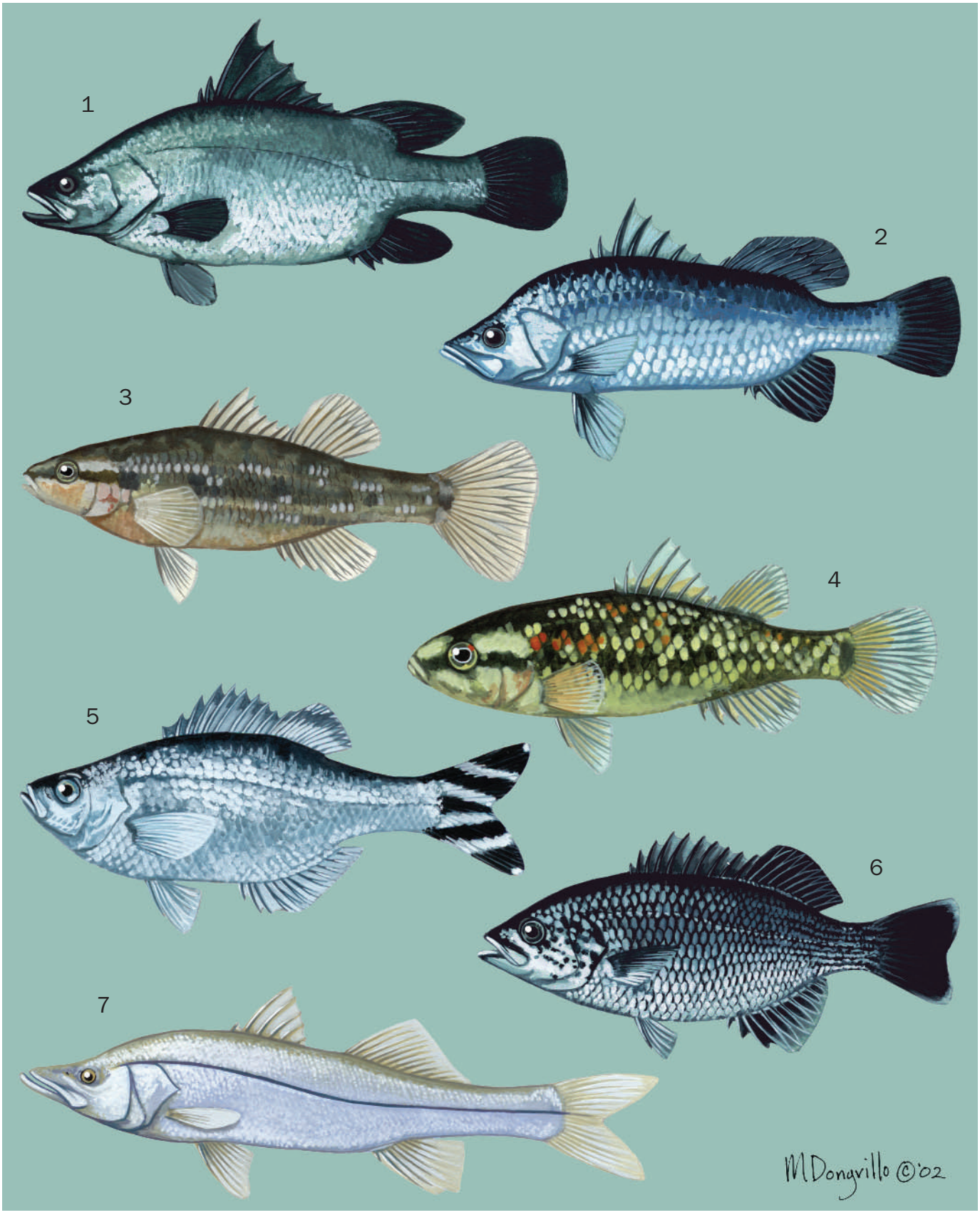
A good number of species of the families Percichthyidae, Gadopsidae, Nannopercidae, and Terapontidae are endemic to specific localities or have relatively small distributions, thus rendering them vulnerable to extirpation or extinction because of habitat destruction, overfishing, or the introduction of exotic species that either compete with or prey upon some life stage of the native species. For example, among the Percichthyidae, the Mary River cod (*Maccullochella peelii mariensis*) is listed as Critically Endangered by the IUCN. The trout cod (*M. macquariensis*) and the Eastern freshwater cod (*M. ikei*) are listed as Endangered. The mountain perch (*Macquaria australasica*) is classified as Data Deficient. In the Nannopercidae, the Oxleyan pygmy perch (*Nannoperca oxleyana*) is listed as Endangered, the Yarra pygmy perch (*N. obscura*) and variegated pygmy perch (*N. variegata*) are listed as Vulnerable. Among the Terapontidae, the silver perch (*Bidyanus bidyanus*), Adamson's grunter (*Hephaestus adamsoni*), and Yamur Lake grunter (*Varia jamoerensis*), are all listed as Vulnerable.

Significance to humans

A number of species are important in commercial, recreational, and subsistence fisheries, while others may be taken incidentally as aquarium fishes. Some species of grunters, temperate basses, and snooks and giant perches are also cultured for food or for release as game fishes. Certain grunters and percichthyids are also utilized in Chinese medicine.



1. Mountain perch (*Macquaria australasica*); 2. Target perch (*Terapon jarbua*); 3. Sooty grunter (*Hephaestus fuliginosus*); 4. Murray cod (*Maccullochella peelii*); 5. Golden perch (*Macquaria ambigua*); 6. Japanese perch (*Lateolabrax japonicus*); 7. River blackfish (*Gadopsis marmoratus*). (Illustration by Marguette Dongvillo)



1. Nile perch (*Lates niloticus*); 2. Barramundi (*Lates calcarifer*); 3. Western pygmy perch (*Edelia vittata*); 4. Southern pygmy perch (*Nannoperca australis*); 5. Flagtail kuhlia (*Kuhlia mugil*); 6. Jungle perch (*Kuhlia rupestris*); 7. Common snook (*Centropomus undecimalis*). (Illustration by Marguette Dongvillo)

Species accounts

Common snook
Centropomus undecimalis

FAMILY
Centropomidae

TAXONOMY
Centropomus undecimalis Bloch, 1792, Jamaica, West Indies.

OTHER COMMON NAMES
English: Robalo blanco; French: Crossie blanc; Spanish: Robalo blanco.

PHYSICAL CHARACTERISTICS
Total length 55 in (140 cm); maximum weight 53.6 lb (24.3 kg). Body relatively large, elongate, and robust. Pronounced sloping forehead and snout. Color silvery with faint olive or greenish hues dorsally, lateral line is black and highly visible. Caudal fin is large and somewhat forked. There are 8–9 spines and 10 soft rays in the dorsal fin, and 3 spines and 6 soft rays in the anal fin.

DISTRIBUTION
Western Atlantic region, in the United States from North Carolina south to Florida, and west along the coast of the Gulf of Mexico coast as far west as Texas; south through several islands in the Caribbean to the coasts of Central and South America, and further south as far as Rio de Janeiro in Brazil.

HABITAT
Shallow coastal marine, brackish, and fresh waters, mainly in estuaries and lagoons and usually in association with mangroves.

BEHAVIOR
Solitary, usually in association with structure but also swims in the water column. Migrates for spawning but will also migrate, for an as yet unexplained reason, into fresh water seasonally.

FEEDING ECOLOGY AND DIET
Prey on smaller benthic and inshore pelagic fishes, as well as crustaceans such as shrimps and crabs.

REPRODUCTIVE BIOLOGY
Maturity occurs in three to five years, with smaller males maturing sooner than larger females. Lives to at least seven years. Fishes migrate seasonally, usually between May to September (but also August to July in Cuba), to estuaries or mouths of passes to court and spawn. Eggs are scattered over the bottom, and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN, but vulnerable to overfishing and habitat destruction.

SIGNIFICANCE TO HUMANS
A very important commercial, subsistence, and game fish. Also raised by aquaculture. ◆

Barramundi
Lates calcarifer

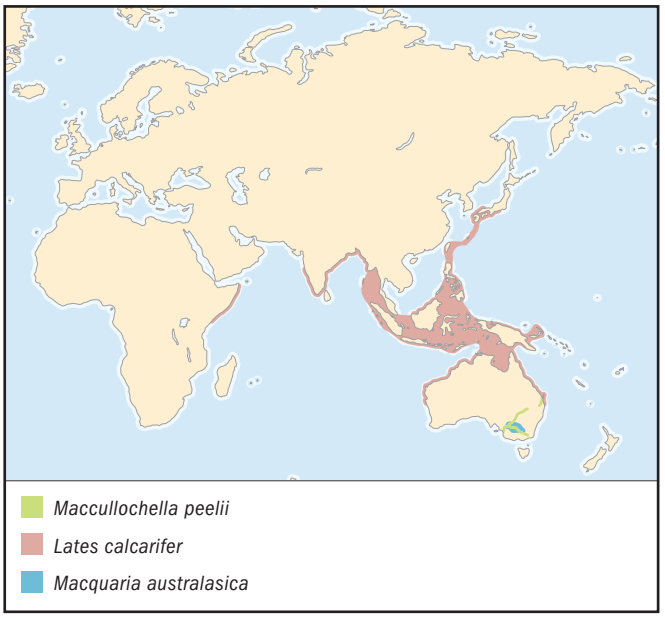
FAMILY
Centropomidae

TAXONOMY
Lates calcarifer Bloch, 1790, Japan.

OTHER COMMON NAMES
English: Asian seabass, Barramundi perch; French: Brochet de mer.

PHYSICAL CHARACTERISTICS
Total length 79 in (200 cm). Body large, elongate, and stout, with pronounced concave dorsal profile in head and a prominent snout. Color silvery but may be greenish or bluish gray on dorsal surfaces. Fins blackish or dusky brown. Juveniles have mottled pattern of brown with three white stripes on head and nape, and white blotches irregularly placed on back. There are 8–9 spines and 10–11 soft rays in the dorsal fin, 3 spines and 7–8 soft rays in the anal fin, and 7–8 soft rays in the pectoral fin. Caudal fin is truncate.

DISTRIBUTION
Indo-West Pacific from East Africa through tropical and warm temperate Asia, including southern Japan, south through Indonesia to northern Australia (from Shark Bay north in Western Australia, and the Mary River in southern Queensland in the east). Insular localities must have sufficient stream development.



HABITAT
Rivers and larger streams, billabongs, submerged floodplains, estuaries, and coastal waters. Juveniles migrate from the ocean upstream to the upper reaches of rivers and creeks where they shelter in vegetation, undercut banks, and other forms of structure. Adults tend to be found in lower reaches of turbid rivers and utilize holes or structure, such as submerged timber, rocks, and mangroves.

BEHAVIOR
Adults and juveniles tend to be solitary, patrol home ranges near structure, and may be territorial. Migration is seasonal.

FEEDING ECOLOGY AND DIET
Voracious predator of fishes and crustaceans. Juveniles also feed on insects. Skilled at stalking or ambushing prey.

REPRODUCTIVE BIOLOGY
Catadromous. Migrates downstream to shallow mudflats in estuaries during the wet season. Spawning occurs between September and March in Australia, with peaks in November to December and again in February to March. Females are larger than males, are highly fecund, and may be courted by one or more males at the same time. Eggs are pelagic, hatch within 24 hours, and the larvae grow quickly as they move into mangrove areas, mudflats, and floodplain lagoons. Juveniles move into coastal waters after one year, then migrate upstream where adults reside for three to four years. Populations landlocked by dams migrate to the dam face, but do not spawn. Raised extensively by aquaculture as food or for game fish-stocking programs.

CONSERVATION STATUS
Not listed by the IUCN, but has been threatened by habitat destruction and overfishing.

SIGNIFICANCE TO HUMANS
Important as a commercial and subsistence food fish but also as a game fish. The most important commercial fish of Australia, and the most sought after game fish, generates millions of dollars per year in revenue for the sportfishing and tourist industries. Cultured fish are replacing wild-caught fishes as food in parts of Australia where netting is banned. Also important in the cultures of aboriginal Australians. ◆

Nile perch
Lates niloticus

FAMILY
Centropomidae

TAXONOMY
Lates niloticus Linnaeus, 1758, Egypt.

OTHER COMMON NAMES
English: African snook; French: Capitaine; German: Nilbarsch; Spanish: Perca del Nilo.

PHYSICAL CHARACTERISTICS
Total length 76 in (193 cm); weight 441 lb (200 kg). Body large, elongate, and robust. Color silvery, with grayish blue along back and grayish silver along flank and belly. Caudal fin and portion of pectoral fin black to dark gray. There are 7–8 spines and 10–14 soft rays in the dorsal fin; the caudal fin is rounded. Free edge of operculum bears a large spine.

DISTRIBUTION
Africa, in fresh and occasionally brackish waters. Present in the Rift Lakes of East Africa, including Lakes Albert, Rudolph, and Tana. Introduced into Lake Victoria and others within and outside of the region, usually with catastrophic results for native fish faunas. Also occurs in major river systems including the Chad (and Lake Chad), Congo, Nile, Senegal, and Volta. Present in Lake Mariout, a brackish water body outside Alexandria, Egypt, near the Nile River.

HABITAT
Large lakes and major rivers and their larger tributaries; also occurs in channels and irrigation canals, brackish-water lakes, and estuaries. Larger adults prefer deeper water, smaller fishes are found in the shallows.

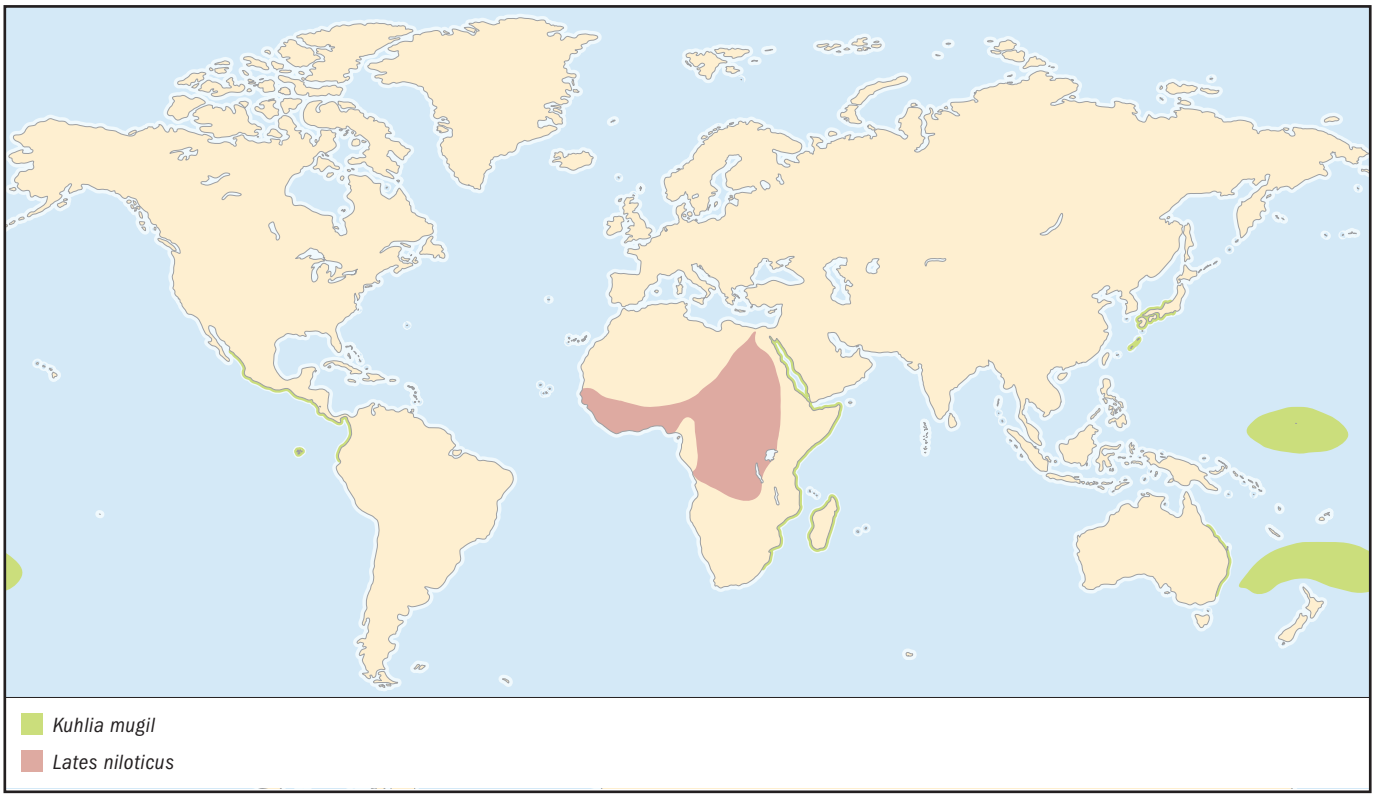
BEHAVIOR
Swims in the water column, but may also associate with structure. Generally solitary.

FEEDING ECOLOGY AND DIET
Highly voracious predator of fishes, especially freshwater herrings in its native range, but also of cichlid fishes. Smaller fishes feed upon crustaceans and insects in shallow water.

REPRODUCTIVE BIOLOGY
Maturity comes in two to three years; larger females reach maturity later than smaller males. The spawning season varies with latitude, temperature, and type of water body, and ranges from February to November, although shorter seasons have been reported. Presumably migrates to a specific site to court and spawn. Eggs are scattered over the bottom or in the water column, and are buoyant. Larvae are pelagic, there is no parental care.

CONSERVATION STATUS
Not listed by the IUCN, but could be vulnerable to commercial overfishing in its native range.

SIGNIFICANCE TO HUMANS
An important commercial and subsistence food fish and game fish, raised by aquaculture for food and stocking. Stocking out-



side its natural range is greatly discouraged. Introduction of this species into Lake Victoria resulted in the decimation of most of a highly diverse and evolved endemic species flock of cichlid fishes, in addition to the loss of other species endemic to that great lake. Similar effects reported elsewhere. ◆

River blackfish
Gadopsis marmoratus

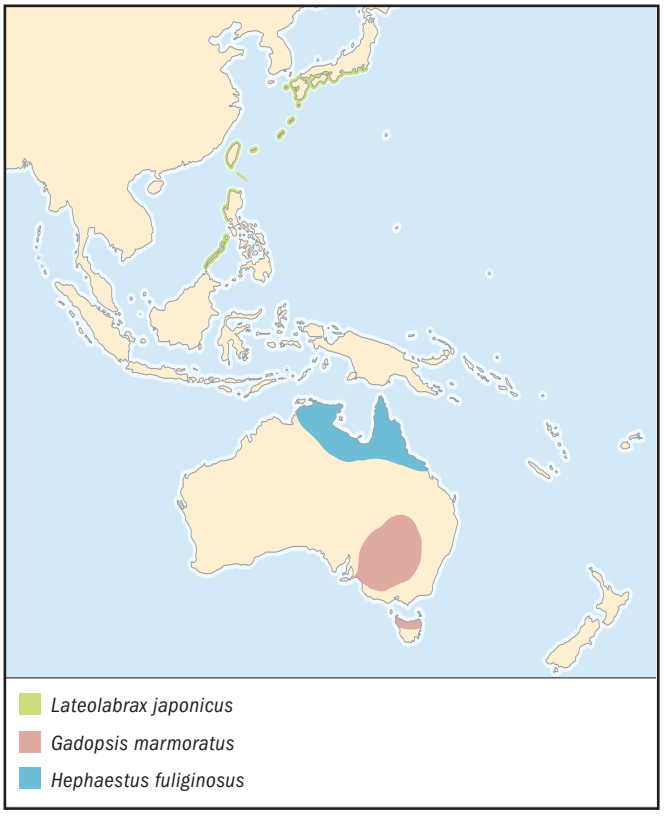
FAMILY
Gadopsidae

TAXONOMY
Gadopsis marmoratus Richardson, 1848, Murray River, and other rivers in South Australia.

OTHER COMMON NAMES
English: Marbled river cod; German: Aalrute, Süßwasserdorsch.

PHYSICAL CHARACTERISTICS
Total length 23.6 in (60 cm) but most, especially in smaller streams, are smaller. Body elongate, slender, and compressed laterally. Snout and caudal fin both rounded. Color is dark gray to pale brown with darker mottling on the flanks and basal portions of fins, with milky or clear color on outer portions of the fins. There are 6–8 spines and 25–28 soft rays in the dorsal fin, 3 spines and 17–19 soft rays in the anal fin, and 15 soft rays in the pectoral fins.

DISTRIBUTION
Murray-Darling River system of Australia, from Victoria into parts of New South Wales, Queensland and South Australia;



also northern Tasmania. Introduced into some rivers of southern Tasmania.

HABITAT
Submerged timber or cover in gently flowing, clear-water streams. Tolerates slightly brackish water in upper tidal reaches of streams. Tolerates extreme temperature ranges from 41–77°F (5–25°C).

BEHAVIOR
Patrols home ranges and is strongly site attached.

FEEDING ECOLOGY AND DIET
Forages for insects, crustaceans, mollusks, and smaller fishes.

REPRODUCTIVE BIOLOGY
Matures in two to three years, females take longer than males. Spawns during austral spring and summer. Female spawns a single, small batch of eggs (20–500 per batch depending upon her size) in a protected place, usually a rock crevice or hollow log within a male's home range. Hatching occurs in about 16 days and larvae remain attached to the egg case for up to 21 more days. The male defends the nest and larvae until they disperse.

CONSERVATION STATUS
Not listed by the IUCN, but vulnerable to habitat destruction and overfishing.

SIGNIFICANCE TO HUMANS
A game fish in the southern portion of its range, but the flesh is oily and not esteemed. May be collected incidentally for aquaria. ◆

Flagtail kuhlia
Kuhlia mugil

FAMILY
Kuhliidae

TAXONOMY
Kuhlia mugil Forster, 1801, Tahiti, Society Islands, Polynesia.

OTHER COMMON NAMES
English: Barred flagtail, flagtail aholehole; French: Croco drapeau; Spanish: Dara bandera.

PHYSICAL CHARACTERISTICS
Standard length 15.7 in (40 cm). Body oval shaped and compressed, the color silver, with black and white markings on the caudal fin. There are 10 spines and 9–11 soft rays in the dorsal fin, and 3 spines and 8–10 soft rays in the anal fin. The caudal fin is forked.

DISTRIBUTION
Widespread in the Indo-Pacific, ranging from the Red Sea and East Africa, including Madagascar, east to the Galápagos Islands, Mexico and Ecuador; also north to southern Japan, and south to Australia and Lord Howe Island. Occurs throughout Micronesia and most of Polynesia as far as Rapa.

HABITAT
Inshore waters along rocky and coral reefs, cliff faces, and rocks. Also enters estuaries and freshwater. Juveniles enter tide pools.

BEHAVIOR
Forms tightly packed schools that swim close to structure, generally just below or in the surge zone.

FEEDING ECOLOGY AND DIET
Feeds upon small swimming crustaceans in the water column.

REPRODUCTIVE BIOLOGY
Not well known. Probably spawns in estuaries or inshore, perhaps in schools, year round in the tropics but seasonally at higher latitudes. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Of minor importance as a commercial and subsistence food fish. Collected for bait and for aquaria. ◆

Jungle perch
Kuhlia rupestris

FAMILY
Kuhliidae

TAXONOMY
Kuhlia rupestris Lacepède, 1802, Gol Ravine, Reunion Island, Indian Ocean.

OTHER COMMON NAMES
English: Freshwater aholehole, freshwater kuhlia, rock flagtail; French: Crocro sauvage; German: Felsen-Flaggenbarsch.

PHYSICAL CHARACTERISTICS
Total length 17.7 in (45 cm), but fishes in upper reaches of freshwater streams are much smaller. Body elongate and robust compared to others in this family. Mouth is relatively large, caudal fin slightly emarginate. Color silvery or light gray with black scale margins, becomes very silvery in marine waters. Caudal fin is either black or clear,with black blotches on each caudal lobe. There are 10 spines and 11 soft rays in the dorsal fin, 3 spines and 9–10 soft rays in the anal fin, and 13–14 soft rays in the pectoral fin.

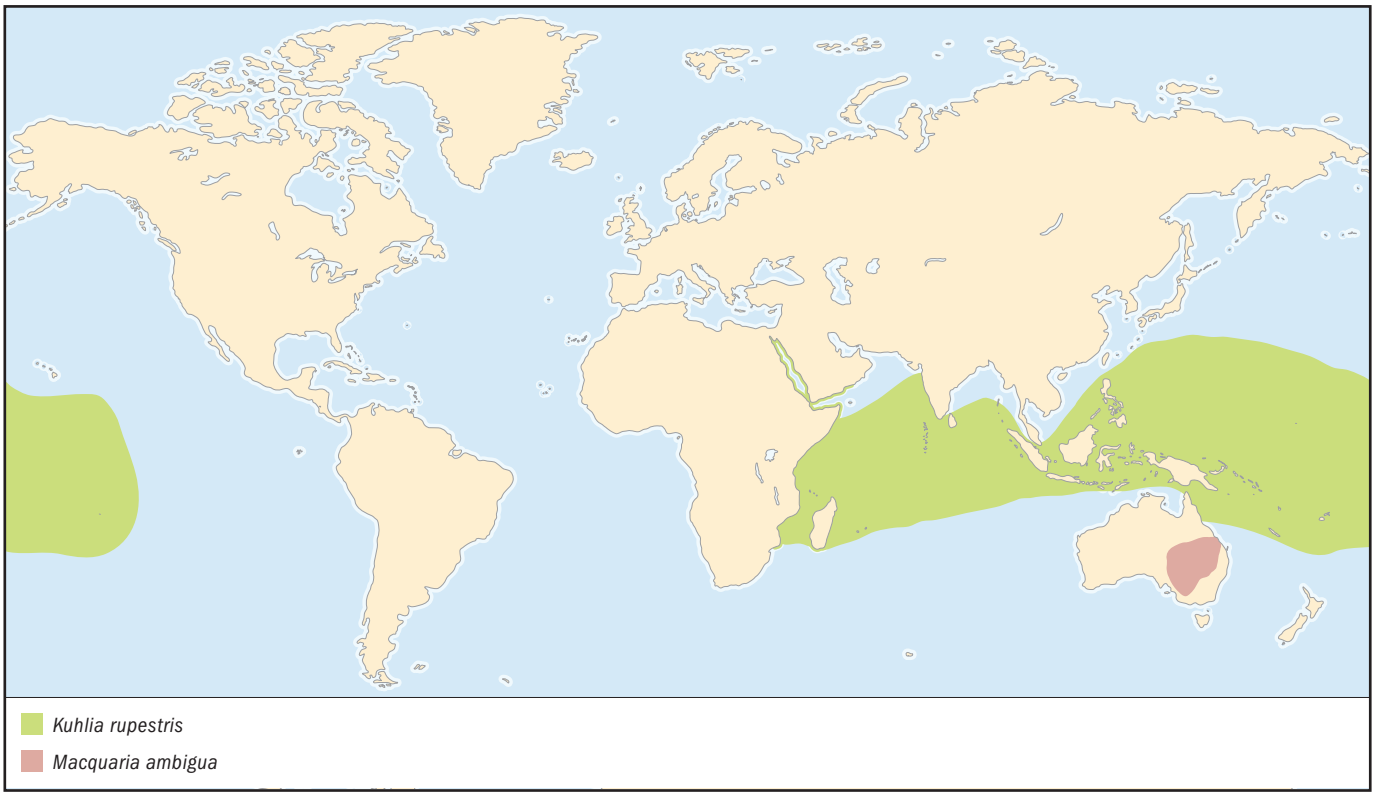
DISTRIBUTION
Indo-West Pacific, from East Africa east to the Ryukyu, Ogasawara, and Mariana Islands, south and east through Micronesia, Melanesia, and Polynesia on islands with freshwater streams; also to Australia as far south as Fraser Island.

HABITAT
Freshwater streams in coastal drainages, usually in clear waters. Also in estuaries and coastal waters seasonally.

BEHAVIOR
Solitary or in small groups in fresh water. Somewhat cryptic in areas with overhanging brush, undercut banks, or other forms of structure.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds upon small fishes, insects, crustaceans, and fruit that falls on the water.

REPRODUCTIVE BIOLOGY
Catadromous, migrates to estuaries on nearshore waters to breed. Behavior not well known. Courtship and spawning



might be in schools or aggregations. Eggs and larvae are pelagic. Post-larvae migrate upstream.

CONSERVATION STATUS
Not listed by the IUCN, but insular populations vulnerable to habitat destruction and overfishing.

SIGNIFICANCE TO HUMANS
Subsistence food fish, may also be taken in minor commercial fisheries. An important freshwater game fish in Australia and esteemed as table fare. ◆

Southern pygmy perch
Nannoperca australis

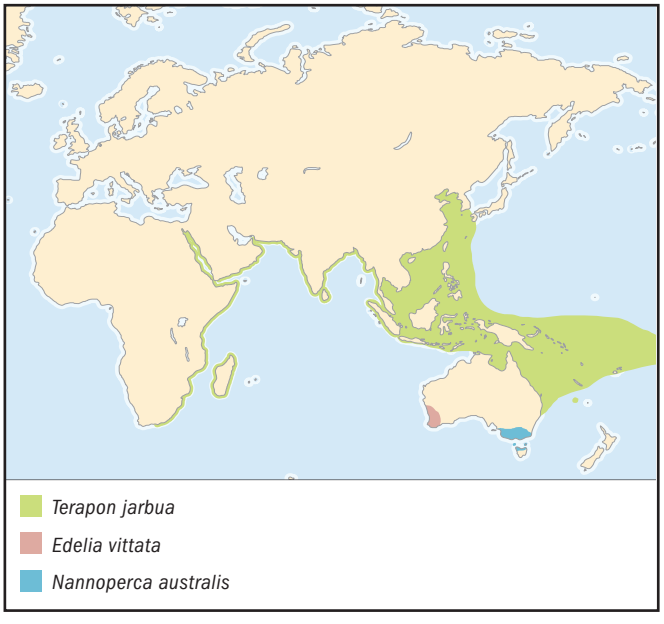
FAMILY
Nannopercidae

TAXONOMY
Nannoperca australis Günther, 1861, Murray River, Australia.

OTHER COMMON NAMES
German: Südaustralischer Zwergbarsch.

PHYSICAL CHARACTERISTICS
Total length nearly 3.5 in (9 cm). Body small and elongate with relatively large, rounded caudal fin. Color silvery or pale gold (occasionally light brown), mottled with a greenish brown hue, the fins are clear. During breeding season, males have hints of orange at base of the dorsal and caudal fins, posterior portion of belly, and above eyes. Pelvic and anal fins are marked with black. There are 7–9 spines and 7–10 soft rays in the dorsal fin, 3 spines and 7–8 soft rays in the anal fin, and 11–14 soft rays in the pectoral fin.

DISTRIBUTION
Australia, generally coastal drainages of Victoria west to mouth of the Murray River in South Australia. Also east to inland reaches of the Murrumbidgee and Murray Rivers in Victoria and New South Wales, and south across Bass Strait to Flinders Island, King Island, and northern Tasmania. The range has contracted because of human interference with natural river flows.



HABITAT
Frequents submerged and emerging shoreline vegetation in streams, drains, billabongs of larger rivers, swamps, and reservoirs. Prefers still or slightly flowing water.

BEHAVIOR
Forms small groups.

FEEDING ECOLOGY AND DIET
Prefers small crustaceans, and larval and adult insects.

REPRODUCTIVE BIOLOGY
Probably matures after the first year and lives as long as five years. Likely moves to preferred spawning sites to spawn demersal eggs in small batches over the course of the season (September to January).

CONSERVATION STATUS
Not listed by the IUCN, but vulnerable to habitat destruction.

SIGNIFICANCE TO HUMANS
May be collected for aquaria or for use as bait. An important prey of introduced species of game fishes. ◆

Western pygmy perch
Edelia vittata

FAMILY
Percichthyidae

TAXONOMY
Edelia vittata Castelnau, 1873, Western Australia.

OTHER COMMON NAMES
German: Westaustralischer Zwergbarsch.

PHYSICAL CHARACTERISTICS
Total length less than 2.75 in (7 cm). Body small and somewhat ovate to elongate. Mouth small, caudal fin relatively large and rounded. Color is mottled, variably olive, brown, or gold with two orange stripes on the flank and a whitish belly. Males assume darker colors dorsally, fins become blackish, flanks mottled gold, and orange stripes deepen during breeding season. Females also change color somewhat during breeding season, assuming a bluish tinge over the bodies. Lateral line interrupted and interspersed with tubed scales. There are 7–9 spines and 8–9 soft rays in the dorsal fin, 3 spines and 6–8 soft rays in the anal fin, and 11–13 soft rays in the pectoral fin.

DISTRIBUTION
Endemic to the southwestern part of Western Australia; common in a number of coastal drainages, from the Philipps River near the city of Albany, north to the Arrowsmith River, about 186 mi (300 km) north of Perth.

HABITAT
Occurs in a variety of permanent water bodies and is somewhat tolerant of slightly brackish or tannin-stained, as well as clear, waters. Shelters in aquatic vegetation along the shorelines of lakes, ponds, wetlands, rivers, and creeks.

BEHAVIOR
Generally solitary in close association with benthic algae.

FEEDING ECOLOGY AND DIET
Carnivore; feeds on benthic microcrustaceans, and adult and larval insects.

REPRODUCTIVE BIOLOGY
Becomes mature after the first year and lives for about five years. Migrates into smaller tributary creeks or submerged floodplains to spawn between July and November. Females lay demersal eggs in small batches for several weeks during the season.

CONSERVATION STATUS
Not listed by the IUCN, but its relatively limited geographic distribution could make it vulnerable to habitat destruction.

SIGNIFICANCE TO HUMANS
May be collected as an aquarium fish and also used to control aquatic insects such as mosquitoes. ◆

Japanese perch
Lateolabrax japonicus

FAMILY
Percichthyidae

TAXONOMY
Lateolabrax japonicus Cuvier, 1828, seas of Japan.

OTHER COMMON NAMES
English: Japanese seaperch, Japan sea bass; Japanese: Suzuki.

PHYSICAL CHARACTERISTICS
Total length 40 in (102 cm). Body elongate, compressed, and perchlike. Mouth is large, lower jaw projects beyond upper jaw. Two dorsal fins. Color silvery but with fine black spots or large black spots on adults from some localities. Juveniles have small black spots on dorsal fin and back. There are 12–15 spines and 12–14 soft rays in the dorsal fin, 3 spines and 7–9 soft rays in the anal fin. Caudal fin is truncate.

DISTRIBUTION
Marine, brackish, and fresh waters of Japan south and west to the South China Sea.

HABITAT
Inshore rocky reefs, usually in moving water. Juveniles enter brackish and fresh waters.

BEHAVIOR
Solitary or in small groups. Will migrate.

FEEDING ECOLOGY AND DIET
Adults and older juveniles feed upon crustaceans, usually prawns and shrimps, and smaller fishes. Younger juveniles feed upon zooplankton.

REPRODUCTIVE BIOLOGY
During winter months, Japanese perch migrate downstream to the sea, join conspecifics migrating from other streams, and spawn on deeper rocky reefs.

CONSERVATION STATUS
Not listed by the IUCN, but may be vulnerable to habitat destruction, particularly in rivers and estuaries.

SIGNIFICANCE TO HUMANS
Commercial fishes and game fishes, also raised by aquaculture and collected for aquaria. Used in Chinese medicine. ◆

Murray cod and Mary River cod
Maccullochella peelii peelii and *M. peelii mariensis*

FAMILY
Percichthyidae

TAXONOMY
Maccullochella peelii peelii Mitchell, 1838, Peel River, New South Wales, Australia. *M. peelii mariensis* Rowland, 1993, Mary River, Queensland, Australia.

OTHER COMMON NAMES
English: Goodo, ponde.

PHYSICAL CHARACTERISTICS
Total length (both subspecies) 80 in (180 cm); weight 250 lb (113 kg). Body large, elongate, and heavy. Body color ranges from olive to cream, occasionally yellowish, with reticulated mottling of dark gray or green along body and onto fins. Fins brownish with white edges, pelvic fin is white. Dorsal fin positioned posteriorly along back. Caudal peduncle of Mary River cod is shorter and the pelvic fins are longer than in Murray cod. Caudal fin is rounded in both subspecies. There are 10–12 spines and 13–16 soft rays in dorsal fin, 3 spines and 11–13 soft rays in anal fin, and 19–20 soft rays in pectoral fin.

DISTRIBUTION
Murray cod: Murray-Darling River system of Australia; absent from upper reaches of these rivers and from the smaller tributaries; its range has shrunk because of habitat destruction. Has been stocked elsewhere. Mary River cod: River Mary in Queensland, Australia, although attempts have been made to establish populations elsewhere, such as the Brisbane River.

HABITAT
Both subspecies favor structure, mainly submerged logs, rocks, or undercut banks, as well as deeper holes in turbid, slow flowing, or clear, rocky reaches of rivers.

BEHAVIOR
Territorial and will defend a piece of habitat, usually a hole or some form of structure. Those in lakes will defend a larger area. Juveniles are migratory.

FEEDING ECOLOGY AND DIET
Carnivorous as adults and older juveniles, feeds upon macroinvertebrates, fishes, amphibians, reptiles, birds, and small terrestrial mammals that enter water. Young juveniles feed upon zooplankton.

REPRODUCTIVE BIOLOGY
Both subspecies mature in about five to six years and may live to 60 years. Courtship and spawning occurs during the austral spring and early summer. Eggs are demersal and guarded by the male. Hatching occurs in one to two weeks to coincide with flooding that brings food for the post-larvae.

CONSERVATION STATUS
The Murray cod is not listed, but is vulnerable to habitat destruction and overfishing. The Mary River cod is classified as Critically Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Culturally important to aboriginal peoples of Australia. Formerly important as commercial species, with overfishing and habitat destruction leading to its decline. The Murray cod is an important but highly regulated game fish. ◆

Golden perch
Macquaria ambigua

FAMILY
Percichthyidae

TAXONOMY
Macquaria ambigua Richardson, 1845, Western Australia (probably an error, although Australia is the correct country).

OTHER COMMON NAMES
English: Yellowbelly, Murray bream; German: Australischer Goldbarsch.

PHYSICAL CHARACTERISTICS
Standard length 29.5 in (75 cm); weight 53 lb (24 kg); most are smaller. Base color is olive, bronze, or brownish, with distinct yellow ventral surface. Body compressed and elongate, but with concave dorsal profile of the head just above eyes, protruding lower jaw, and strongly arched nape. Caudal fin is truncate, pelvic fins have elongate filaments. There are 8–11 spines and 11–13 soft rays in the dorsal fin, 3 spines and 7–10 soft rays in the anal fin, and 15–18 pectoral fin soft rays.

DISTRIBUTION
Lower reaches of the Murray-Darling River system, Dawson-Fitzroy River system in southeastern Queensland, and Bulloo River and Lake Eyre drainages in New South Wales and western Victoria, Australia (the population from the latter locality may be a separate subspecies). Stocked extensively elsewhere, especially in reservoirs.

HABITAT
Turbid, slow-flowing rivers, billabongs, and backwaters, or in clear, fast-flowing rivers. Also in reservoirs. Favors fallen or submerged timber, overhanging banks, and rocky ledges.

BEHAVIOR
Solitary; often associated with structure.

FEEDING ECOLOGY AND DIET
Adults and older juveniles favor macrocrustaceans, mollusks, and smaller fishes; juveniles forage on zooplankton over submerged floodplains.

REPRODUCTIVE BIOLOGY
Females mature in four or more years, males in two to three years. Migrates upstream to spawn and will travel over 1,243 mi (2,000 km) to reach its spawning grounds. Courtship and spawning take place in flooded backwaters. Eggs float after spawning, hatch within 24–36 hours, and larvae disperse downstream. Barriers to migration and corresponding habitat destruction have caused serious declines in recruitment. Cultured artificially for stocking programs.

CONSERVATION STATUS
Not listed by the IUCN, but threatened by habitat destruction.

SIGNIFICANCE TO HUMANS
Mainly a game fish, but a limited commercial fishery exists in the Murray-Darling River system. ◆

Mountain perch
Macquaria australasica

FAMILY
Percichthyidae

TAXONOMY
Macquaria australasica Cuvier, 1830, Macquarie River at Bathurst, New South Wales, Australia.

OTHER COMMON NAMES
English: Black bream, Macquarie perch; German: Macquaries Barsch, Silberauge.

PHYSICAL CHARACTERISTICS
Standard length 17 in (43 cm); maximum weight 7.7 lb (3.5 kg). Base color is dark gray, silvery gray, or olive-brown, and may be mottled; the belly is often pale or light gray, and the scale margins are dark gray. Body is compressed and elongate, the dorsal profile of the head concave, the nape arched, the body deep, the eyes and jaws both large; large mucous cavities are found around the eyes and also on the preoperculum. The dorsal fin has 8–10 spines and 11–14 soft rays; the anal fin has three spines and 8–11 soft rays; there are 14–17 pectoral fin soft rays.

DISTRIBUTION
Middle and upper reaches of Murray River system in New South Wales and Victoria, Australia. Also known from the Yarra River system in Victoria. Introduced elsewhere. A genetically distinct population occurs in the Shoalhaven and Hawkesbury Rivers of New South Wales that may comprise a separate species.

HABITAT
Frequents deep holes on the bottom, but will move up into midwater in streams or reservoirs.

BEHAVIOR
Adults are solitary but form aggregations inshore and when migrating.

FEEDING ECOLOGY AND DIET
Forages for aquatic insects, crustaceans, and mollusks. Post-larvae feed on zooplankton.

REPRODUCTIVE BIOLOGY
Males mature in two years, females in three. Females larger than males. Forms small aggregations that migrate upstream to spawn. Spawning takes place between October and December. Courtship occurs over rocky or gravel bottoms above riffle stretches and demersal eggs are released to scatter onto the bottom; eggs usually slip between interstices of substrate. Eggs hatch in 13–18 days. No parental care.

CONSERVATION STATUS
Classified as Data Deficient by the IUCN. Likely vulnerable to habitat destruction and losses from introduced parasites.

SIGNIFICANCE TO HUMANS
Primarily a game fish, but also a minor component of commercial and aquarium fisheries. ◆

Sooty grunter
Hephaestus fuliginosus

FAMILY
Terapontidae

TAXONOMY
Hephaestus fuliginosus Macleay, 1883, Upper Burdekin River, north Queensland, Australia.

OTHER COMMON NAMES
English: Black bream; German: Rußiger Grunzbarsch.

PHYSICAL CHARACTERISTICS
Reaches 17.7 in (45 cm) total length, but usually smaller in smaller streams. The body is typical of freshwater grunters. Silvery olive in color. There are 11–12 spines and 12–14 soft rays in the dorsal fin, 3 spines and 8–10 soft rays in the anal fin, and 15–17 pectoral fin rays. Lower jaw is distinguished by a discontinuous lip fold.

DISTRIBUTION
Australia, from north coastal Queensland (Cape Hillsborough) to the Gulf of Carpentaria and west to the Daly River in the Northern Territory. Replaced by *H. jenkinsi* in northwestern Australia, including the Kimberly Region of Western Australia.

HABITAT
Sandy or rocky bottoms in the upper reaches of large, flowing streams; also in reservoirs. Tolerates a considerable range of temperatures and moderately acidic conditions.

BEHAVIOR
Solitary or in groups, usually in association with submerged plants or other forms of structure.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds upon invertebrates, amphibians, algae, roots of emergent plants, and fruits that fall upon the water.

REPRODUCTIVE BIOLOGY
Migrates to spawn in groups during summer months; spawning migration is triggered by rains. Eggs are demersal.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Important as a game fish in Australia. ◆

Target perch
Terapon jarbua

FAMILY
Terapontidae

TAXONOMY
Terapon jarbua Forsskål, 1775, Jidda, Saudi Arabia, Red Sea.

OTHER COMMON NAMES
English: Crescent-banded tiger-fish, tiger grunter, tiger perch; French: Peau d'âne, relégué, violon jarbua; Spanish: Baraonga jarbúa.

PHYSICAL CHARACTERISTICS
Total length 14.2 in (36 cm). Body typically perchlike but more elongate. Silvery to light tan in color, with cream on belly and series of black stripes along flank and onto caudal fin. Caudal fin has black tips. There are 11–12 spines and 9–11 soft rays in the dorsal fin, 3 spines and 7–10 soft rays in the anal fin. Lower-most spine on the operculum extends beyond the opercular flap.

DISTRIBUTION
Indo-Pacific, from the Red Sea and East Africa east to Samoa, north to southern Japan, and south to Australia and Lord Howe Island.

HABITAT
Marine and brackish waters, usually in bays, mangroves, and estuaries; will enter rivers. Both adults and juveniles frequent sand flats inshore, but juveniles will enter intertidal zone.

BEHAVIOR
Solitary or in small groups that move about the bottom or around structure.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds upon fishes, insects, benthic invertebrates, and algae.

REPRODUCTIVE BIOLOGY
Catadromous in rivers. Probably spawns in groups in the saltwater. Eggs and larvae are pelagic. Juveniles migrate into lower reaches of rivers.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Minor commercial species also taken in subsistence fisheries; incidental game fishes. Juveniles are collected for the aquarium trade. Also raised in aquaculture. ◆

Resources

Books

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767.
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Percoidei IV

(Goatfishes, butterflyfishes, angelfishes, chubs, and relatives)

Class Actinopterygii
Order Perciformes
Suborder Percoidei
Number of families 18

Photo: A queen angelfish (*Holacanthus ciliaris*) among the coral near Cozumel, Mexico. (Photo by Animals Animals ©Mickey Gibson. Reproduced by permission.)

Evolution and systematics

The suborder Percoidei contains more than 70 families and 2,800 species. This section on the Percoidei deals with 18 families of fishes. The families are the Mullidae (goatfishes), Toxotidae (archerfishes), Dichistiidae (galjoens), Kyphosidae (sea chubs or rudderfishes), Paracorpididae (jutjaws), Drepaneidae (sicklefishes), Monodactylidae (monos or moonfishes), Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Enoplosidae (oldwives), Pentacerotidae (armorheads and boarfishes), Nandidae (leaffishes), Oplegnathidae (knifejaws), Cirrhitidae (hawkfishes), Chironemidae (kelpfishes), Aplodactylidae (seacarps or marblefishes), Cheilodactylidae (morwongs), and Latridae (trumpeters).

Fossil records indicate that perciform fishes date back as far as the Cenozoic era (about 65 million years ago), with percoids evolving rapidly during the Eocene epoch. This rapid evolution is evident in such families as the Chaetodontidae, Pomacanthidae, Mullidae, Kyphosidae, and Cirrhitidae, which contain the most species in the group. A number of families are placed in groups with variable degrees of formalization. For example, the Squammipinnes is an unranked group, denoted by having rows of scales covering the base of the dorsal and anal fins, and includes the Monodactylidae, Toxotidae, Chaetodontidae, and Pomacanthidae. The Kyphosidae consists of four subfamilies, three of which were recognized previously as separate families. (A new molecular study of this polyphyletic group suggests that the subfamilies, which appear to be closely related to the Kuhlidae, might be recognized again as separate families.) The Nandidae also consists of three subfamilies recognized on the basis of their geographical distribution, which parallels the breakup of Gondwana (the supercontinent, made up of South America, Africa, Antarctica, India, and Australia), thus making the nandids an ancient group. Leaffishes have been linked falsely with labyrinth fishes of the suborders Anabantoidei (gouramies and allies) and Channoidei (snakeheads). The superfamily Cirrhitoidea is denoted by the presence of pectoral fins with five-to-eight unbranched and elongated lower fin rays on the pectoral fin. Members include the Cirrhitidae, Chironemidae, Aplodactylidae, Cheilodactylidae, and the Latridae.

Physical characteristics

As with other Percoidei fishes, these fishes are characterized by the presence of spines in the dorsal, pelvic, and anal fins; the presence of two dorsal fins but no adipose fin; the abdominal placement of pelvic fins; pectoral fins that are placed laterally and oriented vertically; the presence of 17 or less principal rays in the caudal fin; and, usually, ctenoid scales (some species possess cycloid scales). These fishes are further characterized by a maxilla that is excluded from the gape of the jaw, a gas bladder that is physoclistous (lacking a connection between the gas bladder and the gut), and bone that is acellular. They also lack four specific bone types: the orbitosphenoid (within the orbital region of the skull), the mesocoracoid (within the pectoral girdle; this bone helps to position the pectoral fin obliquely rather than vertically, as in the percoids), the epileural (riblike intermuscular bones extending below the vertebral column), and the epicentral (primitively ligamentous, riblike intermuscular bones). Body shapes are quite divergent, and range from deep-bodied and highly compressed (Kyphosidae, Drepaneidae, Monodactylidae, Pentacerotidae, Chaetodontidae, Pomacanthidae, and Cheilodactylidae) to elongated (Mullidae) forms. Similarly, there is considerable

Yellowfin goatfishes (*Mulloidichthys vanicolensis*) moving in tight formation over the Dolphin Reef in the Red Sea near Egypt. (Photo by Fred McConnoughey/Photo Researchers, Inc. Reproduced by permission.)

variation in the ecomorphology of the head, jaws, or other structures, both between and within families. Some families, such as the Chaetodontidae, Pomacanthidae, and Cirrhitidae, include many species with brightly colored or highly conspicuous color patterns. Other families (Nandidae) are noted for the cryptic coloration of many species.

Goatfishes are characterized by pairs of long, chemosensory barbels under the lower jaw, a terminal mouth, and the presence of large ctenoid scales. Goatfish larvae are laterally compressed and moderate in depth or elongate. The barbels begin to form at about a length of 0.3–0.35 in (0.8–0.9 cm). Archerfishes have moderately compressed bodies, a pointed head, a dorsal that originates well back towards the caudal fin, and a grooved palate that can direct a stream of water into the air. Their larvae are moderate in depth initially, but become deeper, compressed, and heavily pigmented with age. Galjoens have deep bodies, small ctenoid scales (even on the fins), and a scaleless snout. Sea chubs have a small head with a terminal mouth, a deep and moderately compressed body, a dorsal fin that is continuous, and a caudal fin that is either emarginate (notched) or forked. Their larvae are initially elongate, but become moderate in depth with age, with moderate-to-heavy pigmentation. There is some variation between subfamilies. The jutjaw has an oval-shaped, compressed body, small ctenoid scales, and a large mouth with a projecting lower jaw. Sicklefishes have strongly compressed, oval-shaped bodies covered with cycloid scales and protusile mouths. Monos have deep, highly compressed bodies that are covered with small deciduous scales. Pelvic fins are present in juveniles, but become rudimentary or absent in adults. Their larvae are specialized, having head spination that is moderately developed and elongate pelvic fins that form rather early.

The butterflyfishes have deep, highly compressed bodies; small protractile mouths; somewhat small ctenoid scales; a single dorsal fin that is continuous; and a caudal fin that is rounded or slightly emarginate. The post-larvae have a distinctive *tholichthys* stage, denoted by the presence of bony plates and protruding spines on the head. Angelfishes also have deep, compressed bodies, along with small ctenoid scales, small mouths, and a single dorsal fin that is unnotched. Characters that differentiate angelfishes from the butterflyfishes are a single prominent spine located at the corner of the preopercle; smaller spines on the preopercle, interopercle, and preorbital; and the absence of a *tholichthys* postlarval stage. The oldwife, as an adult, has remarkably large dorsal, pelvic, and anal fins, as well as small ctenoid scales, and a deep, compressed body. Sharp spines are present on the head, anal fin, and dorsal fin; the dorsal spines contain poison and thus the oldwife must be handled with care. Larvae are elongate to moderately long, and are heavily pigmented.

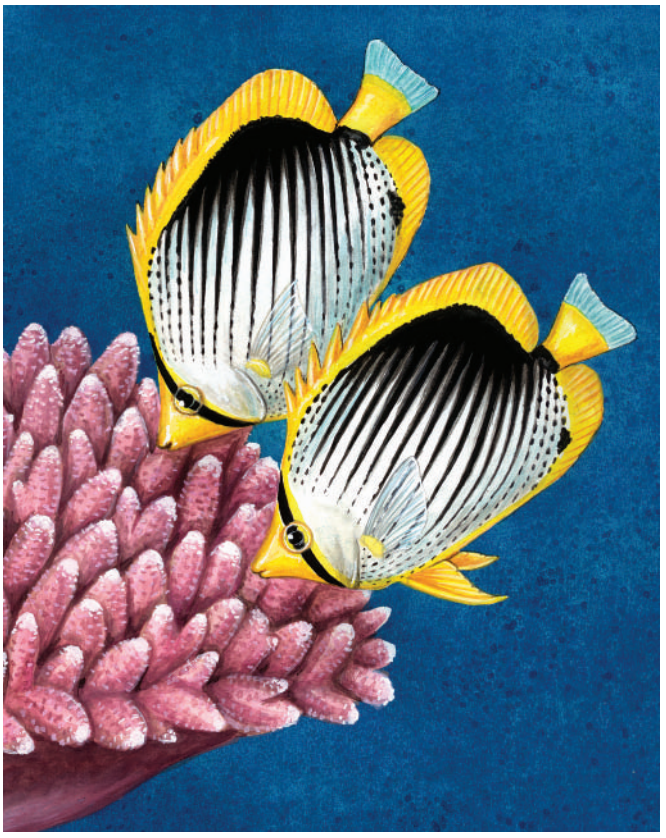
Boarfishes and armorheads resemble the adult oldwife. They have deep, moderately to strongly compressed bodies, exposed head bones that form rough, striated plates, and may have elongated mouths and fin rays. Juveniles may have tall dorsal fins and elongated anal and pelvic fins, but these are reduced as adults. Some species have poisonous spines and should be handled with care. Their larvae are denoted by elongate pelvic fins and extensive, well-developed spination on the head. Leaffishes possess large heads and mouths (the mouth is protactile), continuous dorsal fins, and rounded caudal fins. Knifejaws (Oplegnathidae) have oblong, moderately compressed bodies, tiny ctenoid scales, a single dorsal fin, and a parrotlike beak reminiscent of that on the distantly related parrotfishes (Scaridae). Knifejaw larvae lack subopercular or interopercular spines and are lightly pigmented. Hawkfishes resemble small groupers and their allies (Serranidae) and are characterized by the presence of filaments arranged in small tufts on the tips of the dorsal fin spines and by lower pectoral fin rays that are thickened. Members of the genus *Paracirrhites*, especially *P. arcatus*, *P. hemistictus*, and *P. forsteri*, are polychromatic. Two fixed color morphs occur in the former two species, while the latter exhibits two fixed color patterns in juveniles and a wide range of patterns that have no apparent relationship to sex, adult body size, or geographic locality. However, geographical color variation has been reported for the wide-ranging *Cirrhitus pinnulatus*. Hawkfish larvae have a pigmented chip barbel that disappears with age, cirri on the tips of the dorsal fin spine membrane, and serrations on the preopercle.

Kelpfishes are grouper or hawkfish-like in appearance, with cycloid scales that are moderately large, large pectoral

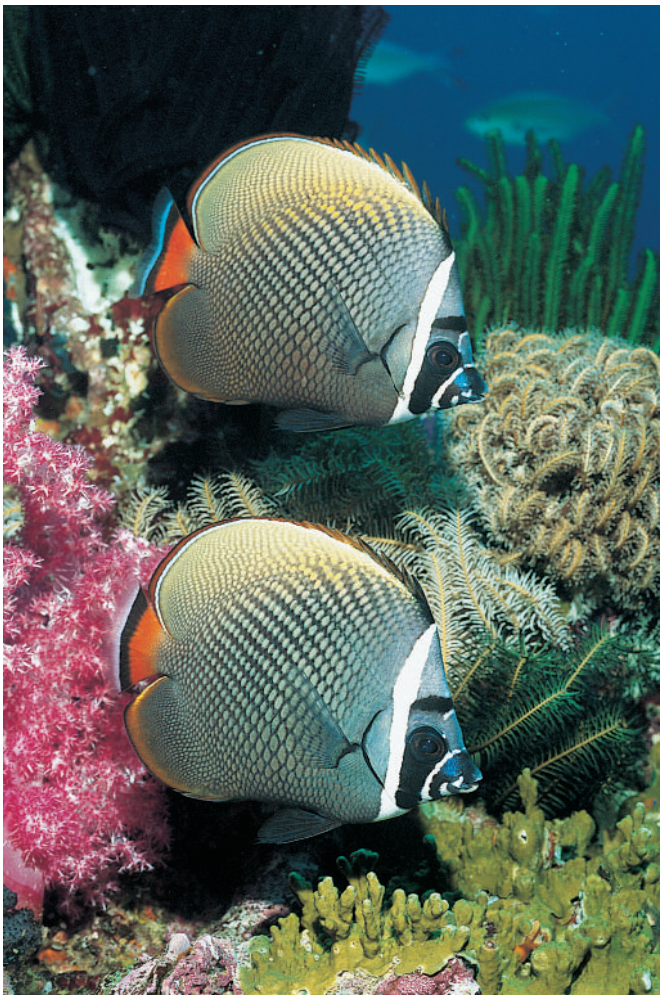
fins, filaments on the tips of dorsal fins, and tufts of filaments on the dorsal spines of some species. Larvae are elongate to moderate in length, lack head spines, have heavy pigmentation in the postflexion stage, and are unspecialized. Sea carps have robust, elongate bodies, small cycloid scales, and pectoral fins with thickened lower rays positioned well forward under the gill covers. Their larvae are long to very elongate, lacking in head spines, heavily pigmented in the postflexion stage, and rather unspecialized. Many morwongs have elongated pectoral rays, forked caudal fins, an elevated dorsal fin, and large rubbery lips. A humplike head and back is present in a number of species. The postlarval stage of morwongs is silvery in color, deep-bodied, and very thin. This stage is retained in most species until they reach 17.7–23.6 in (45–60 cm) in total length. Although somewhat similar in shape to morwongs, the trumpeters have bodies that are elongate and compressed, with small pectoral fins, dorsal fins that are deeply notched, and a protruding mouth. Their postlarval stage resembles that of the morwongs.

Distribution

These fishes occur in coastal and estuarine waters of the Atlantic, Pacific, and Indian Oceans. Some species also occur in freshwater habitats in Africa, Australia, South America, and Southeast Asia. The Mullidae (six genera and 55 species) is found in tropical and warm-temperate coastal waters of the Atlantic, Pacific, and Indian Oceans. The Toxotidae (one genus and six species) is distributed in coastal marine, brackish, and fresh waters of India, east to the Philippines and Vanuatu, and south to northern Australia. The Dichistiidae (one genus and three species) has a distribution limited to coastal and brackish waters in South Africa and Madagascar. The Kyphosidae (15 genera and 42 species) is mostly tropical or subtropical in distribution, but two species have adapted to temperate waters off California. The Paracorpididae (one genus and at least one species) is known from Mozambique and South Africa. The Drepaneidae (one genus and three species) ranges from the Indo-West Pacific to West Africa. The Monodactylidae (two genera and five species) includes popular aquarium fishes found in tropical and warm temperate waters. One wide-ranging species, *Monodactylus argenteus*, occurs in brackish, marine, and freshwater habitats from the Red Sea and East Africa, east to Samoa, north to the Yaeyama Islands of southern Japan, and south to Australia and New Caledonia. A second species, *M. falciformis*, is limited to the western Indian Ocean, from the Red Sea, down to South Africa, and another, *M. kottelati*, is found only at Sri Lanka. *Monodactylus sebae* is found in the eastern Atlantic, from the Canary Islands and Senegal south to Angola. The two remaining species, both in the genus *Schuettea*, are found in temperate brackish and marine waters of southern Australia; one species off southeastern Australia, and the other off Western Australia. The Chaetodontidae (10 genera and as many as 125 species) and the Pomacanthidae (nine genera and at least 73 species) are distributed in tropical, subtropical, and warm temperate coastal waters. Among the chaetodontids, at least 13 species occur in the Atlantic, four species in the eastern Pacific, and the remainder in the Indo-West Pacific region. A similar pattern exists for the pomacanthids. The Enoplosidae (one genus and species) is found in coastal temperate waters of southern Australia. The Pentacerotidae (eight genera and 13 species) occurs primarily in temperate waters of the Indo-Pacific and southwestern Atlantic. The Nandidae (seven genera and 10 species) contains primarily freshwater fishes, but may also occur in brackish-water estuaries. Two species occur in riverine freshwaters of tropical western Africa. *Polycentrus schomburgkii* is found in fresh and brackish water from Trinidad and the Guyanas south to the Amazon Basin, while *Monocirrhus polyacanthus* is found from Guyana south to Brazil and west to the Peruvian Amazon. The remaining species occur from southern Asia east to Southeast Asia, including Indonesia. The Oplegnathidae (one genus and six species) is found in the coastal warm-temperate waters of the Indo-Pacific region, mainly in Japan, southern Australia (including Tasmania), the Galápagos Islands, Peru, and South Africa. One species has also been reported from the volcanic far-northern Mariana Islands. Among cirrhitoid fishes, the Cirrhitidae (12 genera and 33 species) occurs mainly in the Indo-West Pacific region, but also in the tropical and subtropical Atlantic (three species), and eastern Pacific (three species). Two species have distributions that range from the Red Sea east to Mexico and south to Colombia. Three other species range from the Red Sea east to Hawaii and eastern French Polynesia. On the other hand, a number of hawkfishes have limited distributions. For example, the giant hawkfish (*Cirrhitus rivulatus*) is restricted to the Eastern Pacific, including the Galápagos. Similarly, *Itycirrhitus wilhelmi* is found only at Easter and Pitcairn



Mated pair of blackback butterflyfish (*Chaetodon melanotus*) feeding. (Illustration by Joseph E. Trumpey)

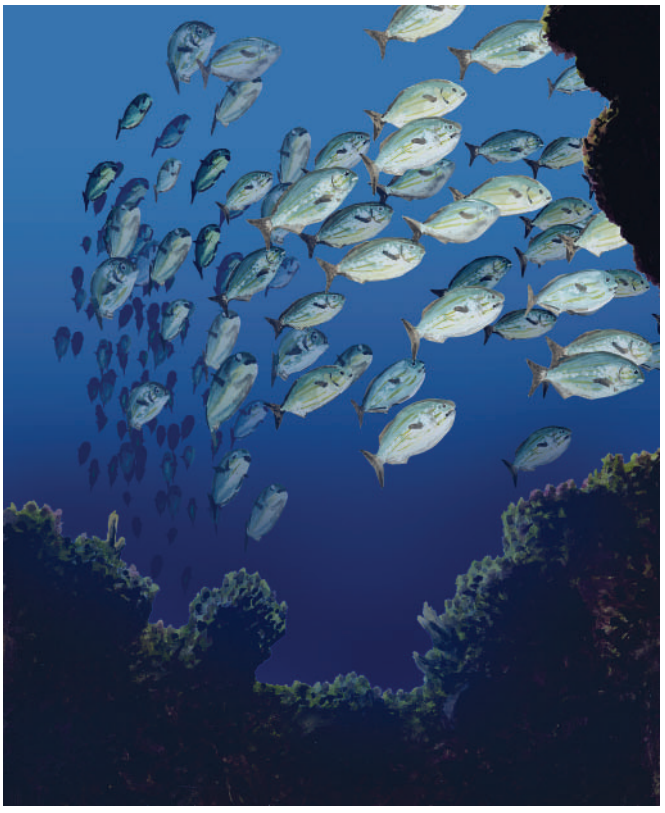


A pair of redtail butterflyfish (*Chaetodon collare*) near the Similan Islands (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Islands at the eastern margin of the central Pacific. The splendid hawkfish (*Notocirrhitus splendens*) is endemic to Lord Howe Island, but strays west to Sydney and the coast of New South Wales in Australia, but also occurs at the Kermadec Islands of New Zealand. The red-barred hawkfish (*Cirrhitops fasciatus*) has a disjunct distribution and is found only in Hawaii, southern Japan, Mauritius, and Madagascar. Another species with a disjunct distribution, *Paracirrhites hemistictus*, occurs sporadically throughout the central and western Pacific, but is also found at Christmas and Cocos-Keeling Islands in the eastern Indian Ocean. The Chironemidae (two genera and four species) is distributed in temperate coastal waters of Australia and New Zealand, with one species endemic to Chile, and another limited to the warm-temperate Lord Howe, Norfolk, and the Kermadec Islands. The Aplodactylidae (three genera and five species) is another Southern Hemisphere family found in the temperate marine waters of Australia, New Zealand, Peru, and Chile. The Cheilodactylidae (four genera and 20 species; *Goniistius* of some authors, treated here as a subgenus of *Cheilodactylus*) has an antitropical distribution. Most species are found in Southern Hemisphere waters (Australia, New Zealand; the Kermadec, Lord Howe, Norfolk, Easter, Rapa, St. Paul's, and Amsterdam Islands; Ilots de Bass, southern Africa, Chile and Peru in the Indo-Pacific; Argentina, southern Africa, Tristan da Cunta Island and Vima Mount in the Atlantic) but members of one genus, *Cheilodactylus*, also occur off Japan, China, and the Hawaiian Islands. Finally, another Southern Hemisphere family, the Latridae (three genera and nine species), is distributed in coastal southern Australia, New Zealand, Chile, and the southern Atlantic.

Habitat

The habitats of these fishes are highly variable, and range from coastal and deepslope or seamount marine habitats, to estuaries, rivers, lakes, ponds, swamps, and even water-filled ditches. Three terms describe the use of these habitats. Benthic fishes are those found in close association with the bottom (including structure); benthopelagic fishes swim on or just above the bottom; and pelagic fishes swim in the water column well above the bottom. Goatfishes are benthopelagic fishes that frequent coral reefs, rocky reefs, and sand, rubble, and mud flats. Archerfishes are pelagic and swim frequently just beneath the surface of shallow marine and brackish waters, and in freshwater lakes and streams. They prefer coastal and estuarine mangroves or weed beds, and flooded trees in freshwaters. Three species are restricted to freshwater habitats. Galjoens are pelagic shoaling fishes found in turbid water along rocky coastlines. Sea chubs are pelagic or benthopelagic, although some pelagic species may be benthopelagic at night. They occur on coral and rocky reefs and frequent high-energy or surge zones. Jutjaws are pelagic fishes of coastal waters. Sicklefishes are benthopelagic in coastal and estuarine waters, and frequent mudflats. Monos are pelagic or benthopelagic, and may frequent mangroves or other structures when not swimming in the water column of bays, back bays, estuaries, or the lower reaches of rivers. Butterflyfishes are either benthopelagic or pelagic over coral reefs (most species), rocky reefs, walls and deep slopes (pelagic species, such as *Hemitaurichthys polycanthus*, that feed on zooplankton), and flats. Juveniles and adults of some species have been reported from mangroves. Similarly, the angelfishes are either benthopelagic or semipelagic, the latter (i.e., *Genicanthus* spp.) moving up into the water column to feed upon zooplankton. A number of benthopelagic angelfishes, such as some members of the genus *Centropyge*, are often found among coral rubble, dead corals, or rocks, where filamentous algae, a component of their diet, is found. Adults of the single species of oldwife (*Enoplosus armatus*) are found on inshore and offshore rocky reefs, and on sea grass beds and in estuaries, but juveniles occur mainly in estuaries. The boarfishes and armorheads are pelagic and occur on deep slopes of inshore reefs, often in or near caves, and seamounts offshore. The leaffishes occur largely in freshwater. All are benthopelagic. Three riverine species are also found in brackish water in estuaries. The most famous leaffish, the *Badis badis*, lives solitarily in rivers, ponds, ditches, and swamps. All leaffishes make use of structure, usually plant materials, for shelter and ambush sites. The knifejaws are found swimming among rocks, underwater cliffs, and walls on rocky reefs. The hawkfishes are benthic, although one species, *Cyprinocirrhites polyactis*, hovers in the



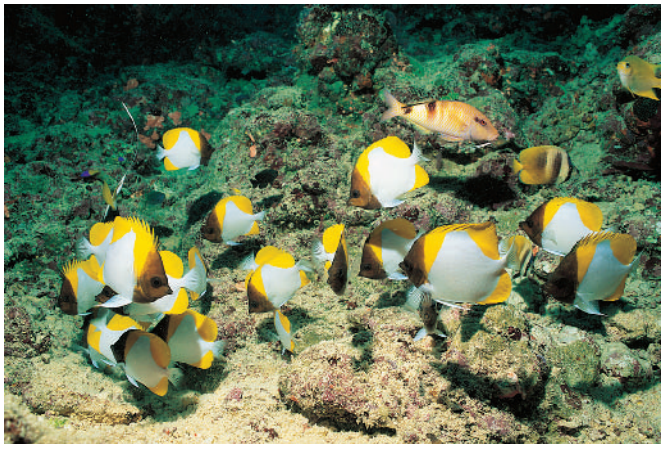
Sea chubs schooling. (Illustration by Brian Cressman)

water column to feed on zooplankton, but darts into holes on the bottom to avoid danger or to shelter for the night. Two species of hawkfishes, *Neocirrhites armatus* and *Oxycirrhites typus*, are obligate coral-dwelling fishes. The former species occurs in shrublike corals of the genus *Pocillopora*, while the latter occurs in gorgonians (sea fans) and black corals found on deep slopes and walls of coral and rocky reefs. Species of the genus *Paracirrhites* are faculative coral-dwelling fishes that shelter in or perch on larger shrub-like corals. If such corals are absent, they will also perch upon coral boulders, ledges and rocks, or hide in holes. Kelpfishes are bottom dwelling, usually in inshore kelp forests, algal beds, and surge zones, or in intertidal reaches of rocky reefs. Seacarps are bottom dwelling and poor swimmers. They are found in small or large loosely maintained aggregations, in surge zones of rocky reefs, and in tidal passes in estuaries. The morwongs occur in a variety of habitats and depth ranges; most species are found on coral or rocky reefs inshore to about 197 ft (60 m), but *Nemadactylus* species have been reported from deep-slope habitats down to 1,312 ft (400 m). The trumpeters occur on rocky reefs and bottoms, although members of the genus *Mendosoma* forage for zooplankton in the water column.

Behavior

There is considerable variety in social organization, locomotion, and other behavior among members of this group. General patterns characteristic of each family are presented here with some greater detail given to certain families. Goatfishes move purposefully along the bottom while foraging and may accompany other bottom-feeding or swimming species for opportunistic feeding, and other fishes, such as wrasses (Labridae), may join them for the same reason. Many goatfishes aggregate in small groups, although members of certain genera, such as *Mulloidichthys* form large schools that seem to hover in the water column when not foraging on the bottom. Others move about singly, however, and some of these, such as *Parupeneus cyclostomus* (a species with two color morphs, golden yellow and pale blue), are remarkably active swimmers. Many species also rest upon the bottom for long periods of time, while some are more active at night than during daytime. The archerfishes use stealth when hunting prey in the manner discussed, but they may be territorial as they move back and forth encountering their neighbors. Galjoens move about in small groups, as do the sea chubs, although the latter can form exceptionally large groups that move about in the water column. The behavior of the jutjaws is poorly known, but they likely form aggregations or schools that swim in the water column. Sicklefishes do the same closer to the bottom. Monos form large schools in the mouths of rivers or in bays, but some occur singly or in small groups under the cover of mangroves in brackish water or brush in freshwater, where some species may be highly territorial.

The behavior of butterflyfishes, perhaps because of their bright coloration and high level of conspicuousness, has been the subject of considerable research. Largely diurnal, butterflyfishes may occur singly and be highly territorial, or live in aggregations with a general home range and relatively little territorial or aggressive behavior. Most, however, may be found in pairs, usually monogamous, that patrol home ranges or protect shared territories. Territorial defense, in general, may be directed towards conspecifics, other butterflyfishes with similar feeding requirements or preferences, or other species of fishes that also share their diet. Species that live singly or in pairs may form aggregations during certain times of the day or season, and these may be related to reproduction. At least one species, *Chaetodon lunula*, which may form aggregations during daytime, is active at night.



Pyramid butterflyfish (*Chaetodon polylepis*) cluster over coral rocks near New Georgia Islands. (Photo by Fred McConoughey/Photo Researchers, Inc. Reproduced by permission.)

Archerfish (*Toxotes jaculatrix*) can spit water up to five feet (1.5 m) to knock insects into the water for a meal. (Photo by Animals Animals ©Stephen Dalton. Reproduced by permission.)

The angelfishes mostly form social and mating groups consisting of a single male and multiple females. They change sex from female to male (protogynous hermaphroditism), usually under social control. Some species may be monogamous or facultatively monogamous. For example, the emperor angelfish (*Pomacanthus imperator*) may often be encountered in pairs that consist of a male and female, yet additional females may reside in the pair's home range and join them prior to courtship at dusk. The regal angelfish (*Pygoplites diacanthus*) is often seen alone, but will form pairs or mating groups during sunset courtship periods. Some intra- and interspecific territorial behavior may occur, usually during encounters while patrolling a home range.

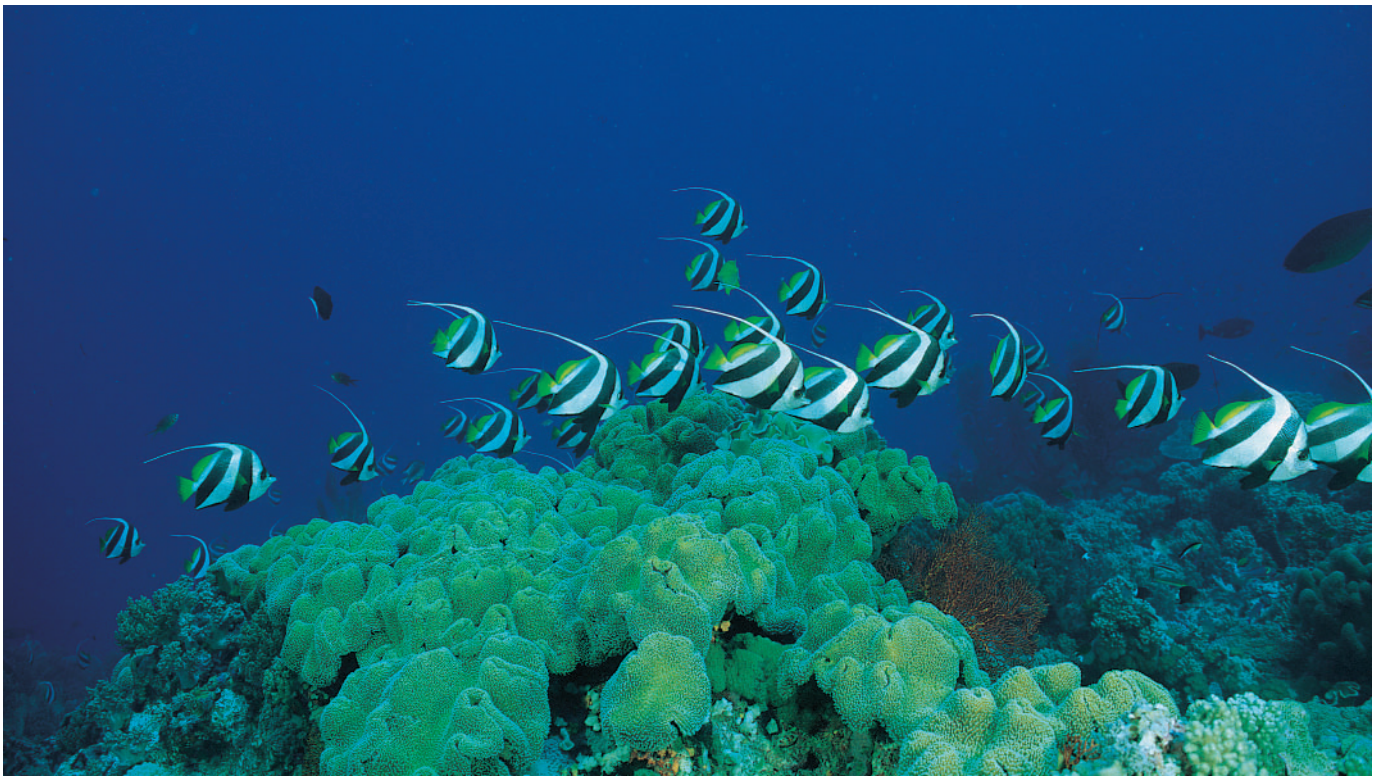
The behavior of the oldwife is not well known. Juveniles occur singly, but tend to form schools as they age. Adults are encountered either singly or in pairs, but large schools may also form. Shallow-dwelling boarfishes occur in pairs or small-to-large aggregations, depending upon the species, but the rarely seen juveniles occur singly. The behavior of their deep-water cousins, the armorheads, is poorly known, but they likely aggregate or form schools. The leaffishes are well known for the way they mimic leaves drifting in the water column. This allows them to avoid predation and to ambush potential prey. Little is known about the behavior of knifejaws except that they swim about rocks and will enter caves.

The hawkfishes are territorial and organized socially into mating groups consisting of a single male and a variable number of females (usually two to five) that maintain territories or home areas inside the male's territory. Two species, however, are facultatively monogamous as a consequence of habitat use. For example, obligate coral-dwelling species, such as *Oxycirrhites typus* and *Neocirrhites armatus*, are facultatively monogamous if their coral (black coral or gorgonian sea fan, in the case of *O. typus*) is too small to support more than two fish, and if neighboring corals are too far away to allow a male to safely move to it to court a resident female. However, if the coral is large enough to support more than two fishes, or if suitable corals are close by, then a multiple-female group is possible. Juvenile obligate coral-dwelling hawkfishes often recruit to less-favorable corals nearby and then attempt, as do facultative and noncoral-dwelling species, to gain entry into the mating group. Usually, resident females will attack the new arrival and try to expel it from the coral or the group. This behavior is also directed towards adults, usually emigrants from fragmented groups elsewhere, that attempt to join the group. If the emigrant is recognized as another male, the resident male will attempt to expel it; if a female, it may be attacked by other females. As with other fishes that have a similar social organization, all hawkfishes likely change sex from female to male (protogynous hermaphroditism). Sex change may proceed through social control or maturation. The effect of sex change upon social organization can be profound, because, in addition to allowing for succession by the dominant female with the loss of the male, it can also allow the dominant female to fragment the group should it become too large for the male to control effectively. Similarly, if the dominant male cannot control his group, then neighboring males and "rogue" males (those that have lost a group or were recent females that could not fragment their own group after changing sex) can attempt to sequester females. Another interesting behavior is practiced by the plankton-feeding *Cyprinocirrhites polyactis*, which mimics fairy basslets (Serranidae: Anthiinae) that aggregate, often in considerable numbers, in the water column.

Kelpfishes may establish large aggregations that form loosely over reefs, particularly surge zones, but individuals and small groups are more likely in the intertidal zone. The seacarps also aggregate, either in small or large, loosely organized groups that rest upon the bottom. They swim with the dorsal fin raised when seeking food or changing location. Most morwongs move about the bottom singly or in small, loosely formed aggregations, but members of the genus *Nemadactylus* form large aggregations. Trumpeters are mostly schooling fishes, which move about in small groups or in aggregations of hundreds of individuals.

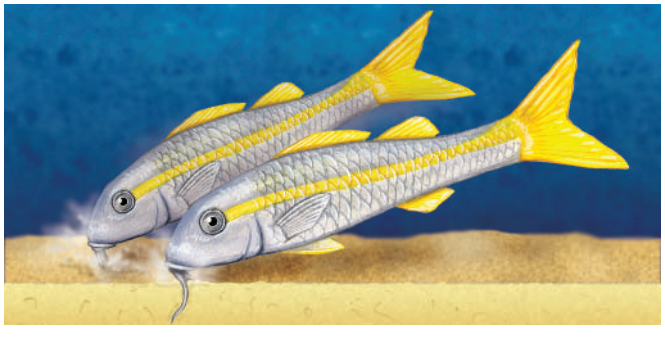
Feeding ecology and diet

These fishes have considerable variation in both feeding methods and diet. Although most direct their attention towards bottom feeding or planktivory, in which they feed upon phytoplankton or zooplankton in the water column, there are some remarkable exceptions. Goatfishes utilize their barbels, which bear chemosensory organs, to stir up the bottom and



Schooling bannerfishes (*Heniochus diphreutes*) feed on plankton and are widespread in the tropical Indo-Pacific. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

detect prey. They also feed upon smaller invertebrates in sand, rubble, algal beds, or on coral pavement, and some species may take small fishes that they disturb. Archerfishes swim near the surface of the water and can detect visually, with a correction for light refraction, terrestrial prey on overhanging branches of trees and shrubs or blades of grass at the water's edge. Upon detecting the prey, usually an insect, archerfishes direct a stream of water drops toward that prey, knocking it to the water where it can be captured with the mouth and consumed. The drops are formed by compression of water by the gill covers and shot by forcing them along a groove formed by the tongue and palate. Archerfishes also consume floating fruits and flowers. Although galjoens have small mouths, they are capable of preying upon ascidians, mussels, barnacles, and other crustaceans. Galjoens also consume seaweeds. The sea chubs have a mixed feeding strategy and diet. Members of the subfamilies Kyphosinae (except the genus *Gras*) and Girellinae graze or pluck algae. Those in the subfamilies Scorpidinae and Microcanthinae are carnivores that feed upon benthic invertebrates. The jutjaws strain zooplankton from the water column. The sicklefishes feed upon small invertebrates they extract from soft sediments, usually mud. Monos have small, obliquely positioned mouths with a combination of brushlike teeth on their jaws, villiform teeth on the vomer, and palatines within the mouth. They use this combination to capture and feed upon small fishes, invertebrates, or plankton. The butterflyfishes have been collectively described as microconsumers. Some species feed exclusively upon coral polyps, others upon small invertebrates on corals, rocks, coral pavement, or crevices, and still others, such as *Hemitaurichthys polylepis*, forage for zooplankton in the water column. There is some plasticity in diet for a number of species. While *Chaetodon trifascialis* feeds only upon acroporid corals, *C. punctatofasciatus* will feed upon a variety of benthic invertebrates, corals, and even filamentous algae. The forcepsfish (*Forcipiger flavissimus*) uses its tubular snout to feed upon hydroids, fish eggs, and small crustaceans, and to excise pieces of the tentacles of polychaete worms, the tube feet of starfishes, and the pedicilaria of sea urchins. On the other hand, the longnose butterflyfish (*F. longirostris*), with its longer snout, feeds mainly upon small crustaceans that are taken whole. Angelfishes also



A pair of yellow goatfish (*Mulloidichthys martinicus*) foraging in bottom sediments for food. The barbels situated under their chins have chemosensory organs that allow goatfishes to detect potential prey. (Illustration by Joseph E. Trumpey)

A juvenile emperor angelfish (*Pomacanthus imperator*) near Gavutu Island, in the Solomon Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.

have considerable plasticity in their diet, although perhaps less so compared to butterflyfishes. Pygmy angelfishes (*Centropyge* spp.) feed mostly upon filamentous algae, while *Genicanthus* angelfishes forage mainly for zooplankton in the water column and supplement their diet with benthic invertebrates or algae. Others in the family feed upon sponges, small soft-bodied invertebrates, fish eggs, and algae.

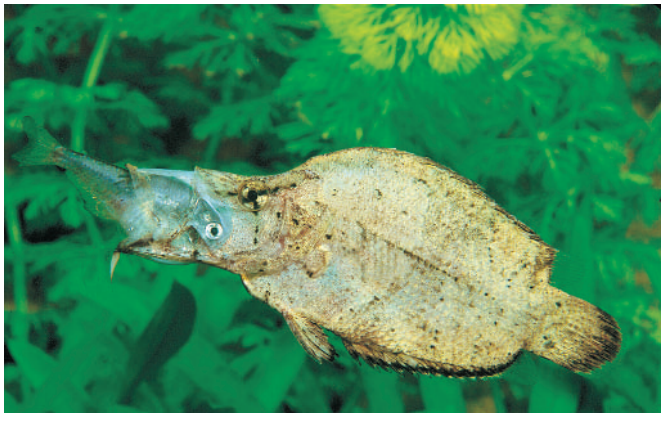
Little is known about the feeding habits and diets of the oldwife, boarfishes, and armorheads, but they appear to feed upon benthic invertebrates and fishes. Leaffishes, which can conceal themselves even in open water thanks to their ability to mimic leaves downed in water, are remarkably good predators upon fishes and invertebrates (mostly crustaceans, insects, and worms). However, one larger species from Southeast Asia, the catopra (*Pristolepis fasciata*), is primarily a herbivore that feeds upon filamentous algae, submerged land plants, seeds, and fruits, but will also take crustaceans and aquatic insects. Knifejaws use their parrotlike beaks to break open and feed upon barnacles and mollusks. The hawkfishes feed upon small crustaceans and fishes they ambush from a perched position on a coral or rock, or from a resting position on the bottom. One species, *Cyprinocirrhites polyactis*, plucks zooplankton while hovering in the water column, and a second species, *Cirrhitichthys aprinus*, has been observed taking zooplankton as it darts out from soft corals into the water column along current-swept reef walls. Kelpfishes exhibit feeding behavior similar to hawkfishes and feed upon small invertebrates. The seacarps feed upon algae and other seaweeds they grab from the bottom with their mouths. The small mouths and thick lips of morwongs are used to feed upon small benthic or pelagic invertebrates, such as polychaete worms, crustaceans, mollusks, and echinoderms, or in some species, algae. At least one species, *Chirodactylus grandis*, feeds upon squid and small fishes. Trumpeters feed upon benthic invertebrates, although the members of the genus *Mendosoma* feed upon zooplankton.

Reproductive biology

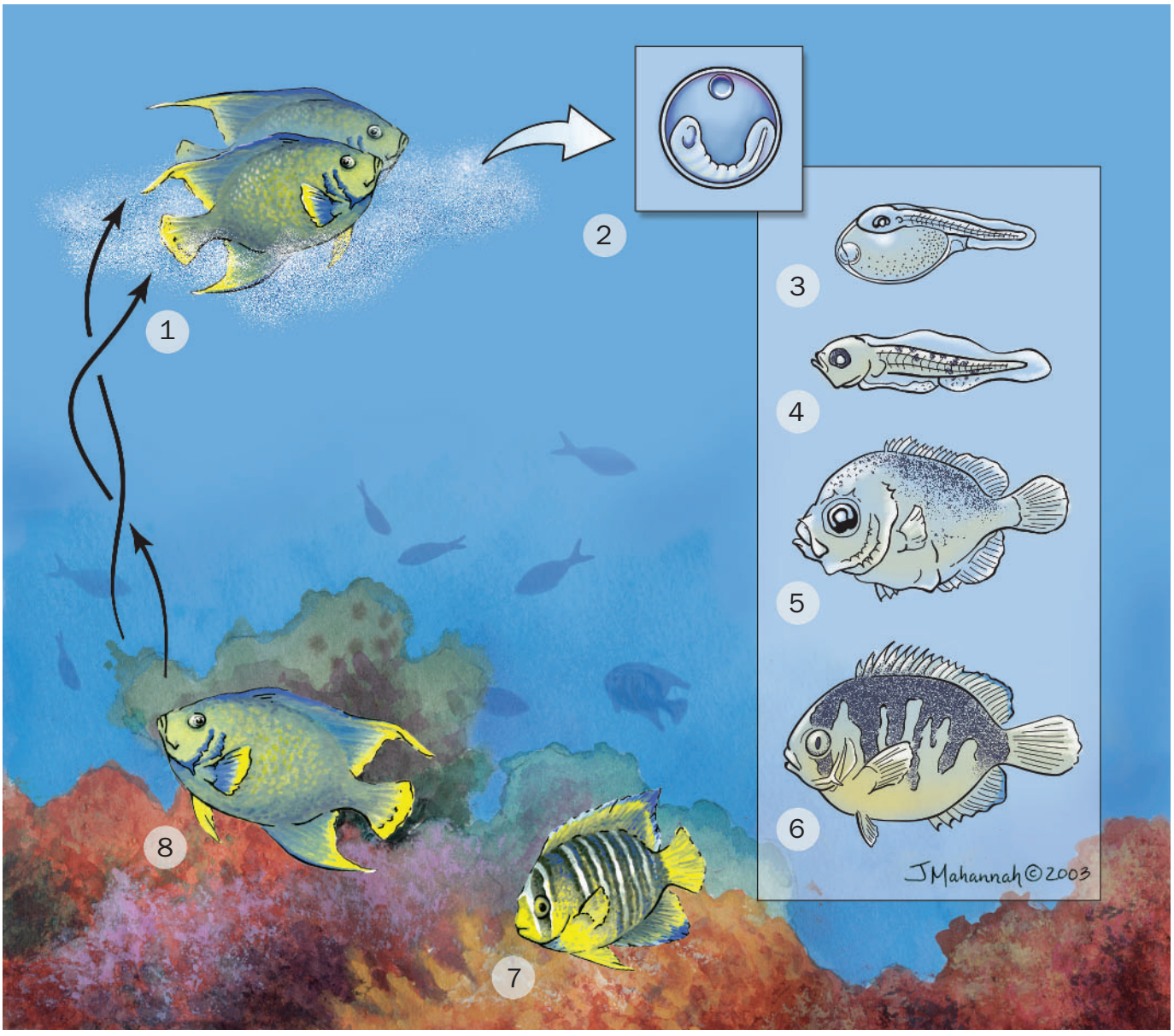
Although studies on reproductive biology of these fishes are far from complete, there is considerable information, which characterizes some families in detail. Overall, they are either gonochorists or sequential hermaphrodites. Gonochoristic fishes begin life either as females or males and remain that way their entire lives. Examples include goatfishes, archerfishes, galjoens, sea chubs, jutjaws, sicklefishes, monos, butterflyfishes, the oldwife, boarfishes and armorheads, leaffishes, knifejaws, and morwongs. Sequential hermaphrodites change sex. Most Percoidei with this life strategy appear to be protogynous hermaphrodites, in that they begin as females but may change sex and become males. The control of sex change may be social or as a consequence of maturation, and despite detailed research on some groups (i.e., angelfishes and hawkfishes), much remains to be learned about the circumstances that trigger sex change. The status of kelpfishes, seacarps, and trumpeters is uncertain.

Spawning may occur in monogamous pairs, as sequential pairs within a haremic mating group or spawning aggregation, or promiscuously. Most of these fishes appear to spawn pelagically, the eggs are fertilized in the water column during pair spawning, and there is no parental care. Sneaking (partial fertilization of a pair's eggs by a second male that sneaks up on a rising pair) and group spawning are also possible. Pelagic spawning has been verified for the goatfishes (paired and group spawning), archerfishes, sea chubs, monos (in part), butterflyfishes, angelfishes, the oldwife, hawkfishes, morwongs, and trumpeters. Pelagic spawning is presumed in the galjoens, jutjaws, sicklefishes, boarfishes and armorheads, knifejaws, kelpfishes, and seacarps. Demersal spawning, in which eggs are scattered on the bottom, placed in nests or bubble nests (a specialized behavior of some leaffishes), brooded in holes or caves, or attached to plants, shells, rocks, or some form of structure, may involve parental care to some degree or not at all. Parental care is pronounced, especially in freshwater fishes such as the leaffishes, but is largely absent or minimal in marine fishes. Leaffishes spawn demersally, or in bubble nests, and some monos also have demersal eggs.

There is considerable variability in the temporal patterns of spawning of these fishes. They may spawn only seasonally in relation to latitude and water temperature but not exclu-



An Amazon leaffish (*Monocirrhus polyacanthus*) eating a smaller fish. (Photo by Animals Animals ©M. Gibbs, OSF. Reproduced by permission.)



The life cycle of a reef fish, the blue angelfish (*Holacanthus bermudensis*). 1. A pair spirals toward the surface, where eggs are released; 2. Pelagic fertilized egg with single oil droplet; 3. Newly hatched larva, 0.06 in (1.58 mm); 4. 0.10 in (2.5 mm) larva; 5. 0.17 in (4.2 mm) larva; 6. 0.5 in (13 mm) post-larva; 7. Juvenile; 8. Adult. (Illustration by Jacqueline Mahannah)

sively. For example, fishes of some families might spawn seasonally over a short period of time once or twice a year regardless of latitude. Others, such as the hawkfishes, may spawn daily at lower latitudes, but seasonally at higher latitudes. Those fishes that produce pelagic eggs and larvae have the potential for relatively long-distance dispersal in marine systems. Demersally spawned eggs usually also hatch to become pelagic larvae, but these may not disperse as far. Of course, there are plenty of exceptions to the rule in both cases.

Conservation status

One species of angelfish (*Centropyge resplendens* [Pomacanthidae]), and five species of butterflyfish (*Chaetodon flavocoronatus*, *C. litus*, *C. marleyi*, *C. obliquus*, and *C. robustus* [Chaetodontidae]) are listed as Vulnerable on the IUCN Red List. Other species may be vulnerable or threatened, but the data simply do not exist to verify the conservation status of many of these fishes. Certainly, species that live in close association with corals (such as butterflyfishes, angelfishes, and hawkfishes) might be at risk because of the effects of coral bleaching, the harvest of corals, and the general destruction of coral habitats. The same might be said of species that live in mangroves (such as archerfishes) threatened with destruction. The leaffishes may be at risk from the effects of pollution, hydroelectric development, so-called stream improvements, the draining of swamps, destructive agricultural practices, mining, logging, and other forms of development that contribute to the

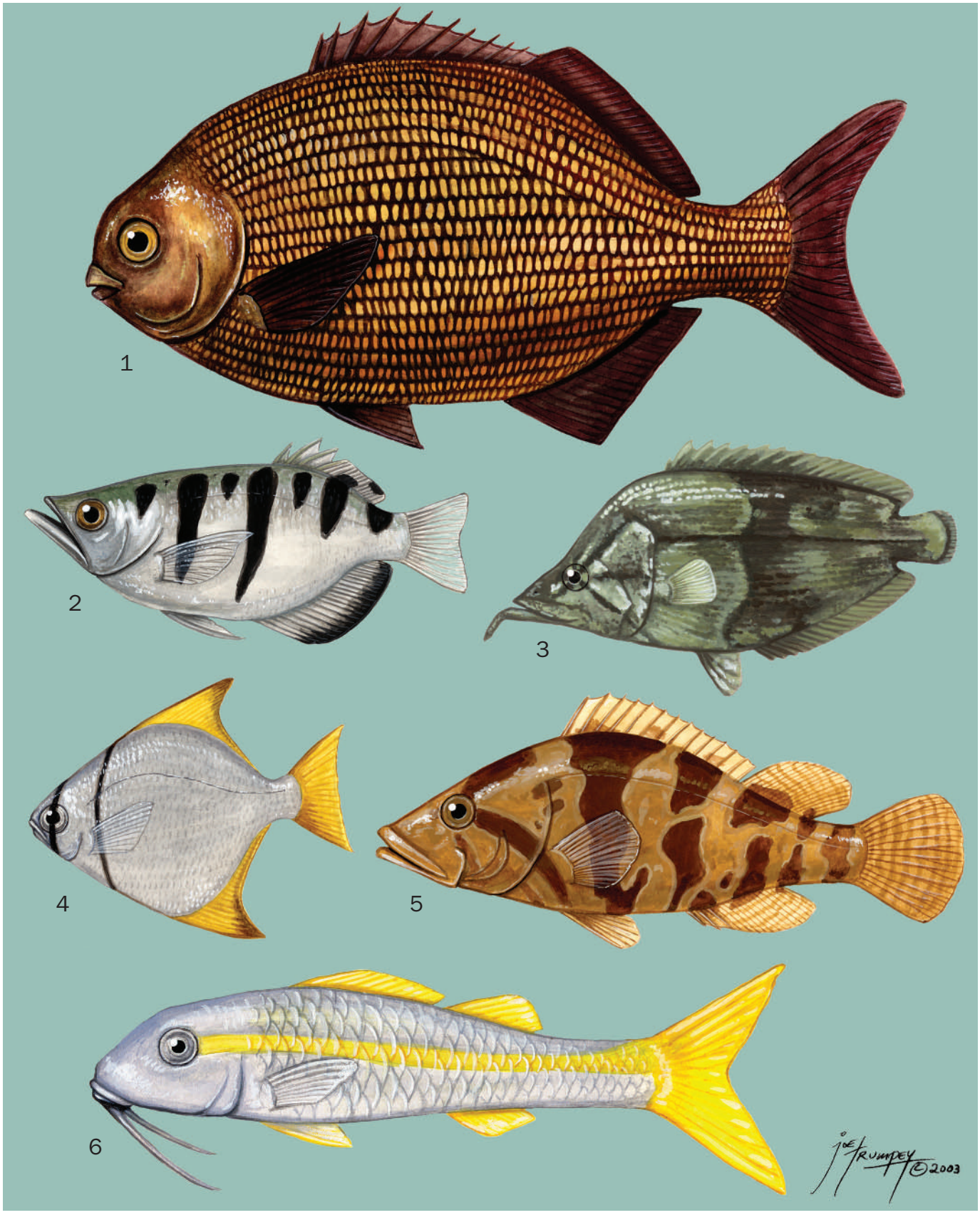
A pair of red goatfish (*Mullus surmuletus*). (Photo by Tom McHugh/ Photo Researchers, Inc. Reproduced by permission.)

sedimentation of rivers and streams. Galjoens require considerable protection from overfishing in South Africa. Similarly, armorheads that dwell on seamounts or on deep-slope reefs and grounds are likely candidates for overfishing and should be of considerable concern. Overfishing of popular aquarium species (such as leaffishes, butterflyfishes, angelfishes, and hawkfishes), especially those that are rare, have limited distributions locally or geographically, or have mating systems or other life history characteristics that make them especially vulnerable to unregulated harvests, is also of great concern.

Significance to humans

Fishes of the following families are taken in major or minor commercial food fisheries: Mullidae, Parascorpididae, Enoplosidae, Pentacerotidae, Oplegnathidae, Cheilodactylidae, Chironemidae, and Latridae. Fishes that may be found in subsistence food fisheries include the Mullidae, Toxotidae, Kyphosidae (prized at some localities but avoided at others), Monodactylidae, Chaetodontidae, Pomacanthidae, Nandidae, larger Cirrhitidae, and Cheilodactylidae. Game fishes include members of the Dichistiidae (their numbers heavily depleted in South Africa), Nandidae, Oplegnathidae, Cheilodactylidae, and the Latridae. Some members of the Chironemidae and Aplodactylidae are not taken generally for food because they apparently taste bad. A number of families are taken for the aquarium trade, either as juveniles or adults. Important species include members of the Toxotidae, Nandidae, Monodactylidae, Chaetodontidae, Pomacanthidae, and Cirrhitidae. Of minor importance are members of the Mullidae, Kyphosidae, Enoplosidae, and Cheilodactylidae.

1. Pebbled butterflyfish (*Chaetodon multicinctus*); 2. Adult emperor angelfish (*Pomacanthus imperator*); 3. Juvenile emperor angelfish; 4. Hawaiian morwong (*Cheilodactylus vittatus*); 5. Longnose hawkfish (*Oxycirrhites typus*); 6. Striped boarfish (*Evistias acutirostris*). (Illustration by Joseph E. Trumpey)



1. Cortez chub (*Kyphosus elegans*); 2. Banded archerfish (*Toxotes jaculatrix*); 3. Amazon leaffish (*Monocirrhus polyacanthus*); 4. Mono (*Monodactylus argenteus*); 5. Gangetic leaffish (*Nandus nandus*); 6. Yellow goatfish (*Mulloidichthys martinicus*). (Illustration by Joesph E. Trumpey)

Species accounts

Pebbled butterflyfish
Chaetodon multicinctus

FAMILY
Chaetodontidae

TAXONOMY
Chaetodon multicinctus Garrett, 1863, Hawaiian Islands.

OTHER COMMON NAMES
Hawaiian: Kikakapu.

PHYSICAL CHARACTERISTICS
Deep, compressed body, whitish in color, with four to six narrow brown or gold-brown bars and many faint olive spots on both the body and the fins; a gold-brown eye bar on the head, a black and gold bar on the caudal peduncle, and a solid black bar on the caudal fin. To 4.5 in (12 cm) total length.

DISTRIBUTION
Limited to the Hawaiian Islands and Johnston Atoll in the east-central Pacific.

HABITAT
Seaward or lagoon coral reefs, usually with considerable stands of *Porites* and *Pocillopora* corals, between 16 and 98 ft (5–30 m) in depth.

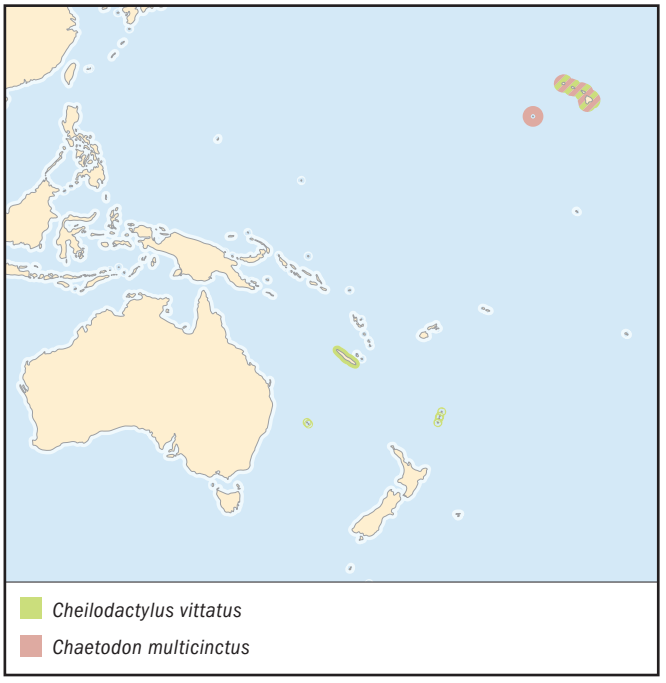
BEHAVIOR
Forms heterosexual pairs but occasionally occurs in small aggregations.

FEEDING ECOLOGY AND DIET
Omnivorous, its diet consisting of coral polyps, polychaete worms, small crustaceans, and algae.

REPRODUCTIVE BIOLOGY
Gonochoristic. Paired courtship just before or after sunset into early evening, with pelagic spawning in the water column. Spawning pairs are occasionally joined by one or more intruding males who attempt to spawn with the female. The intruders may be either rogue males or paired males who have temporarily abandoned their mates. Courtship occurs between December and July, but courtship and spawning is most pronounced between March and July. Eggs and larvae are pelagic. The eggs are spherical and small (0.023–0.029 in [0.6–0.75 mm] in diameter). Larvae are around 0.059 in (1.5 mm) in length at hatching and have a large yolk sac. The mouth is unformed and the eyes are unpigmented. With growth, the larva develops fused head plates that extend over the trunk of the body. This is known as the thoichthys stage of development; it adapts the larva to a long pelagic phase. Other adaptations include spine formation on the head, dorsal, and pelvic fins.

CONSERVATION STATUS
Not listed by the IUCN. Coral habitats may be threatened by coral bleaching, pollution, sedimentation, and other forms of degradation that may negatively impact populations of this limited-distribution species.

SIGNIFICANCE TO HUMANS
May be collected for the aquarium trade, but this and many other butterflyfishes generally do poorly in most aquaria. ◆



Hawaiian morwong
Cheilodactylus vittatus

FAMILY
Cheilodactylidae

TAXONOMY
Cheilodactylus vittatus Garrett, 1864, Hawaiian Islands.

OTHER COMMON NAMES
Hawaiian: Kikakapu.

PHYSICAL CHARACTERISTICS
Laterally compressed with a high forehead and long, sloping back. There are prominent bony knobs on the head. The caudal fin is forked. There is an oblique pale black bar on the head, and there are four oblique dark-black bars, all against a white background color, along the head and flank. The dorsal fin spines are black, white, and orange-red; the dorsal rays are white.

DISTRIBUTION
Hawaiian Islands in the Northern Hemisphere, and New Caledonia, Lord Howe Island, and the Kermedec Islands in the Southern Hemisphere.

HABITAT
Coral and volcanic rocky reefs, in areas of coral, rocks, pavement and rubble. Depth usually below 65 ft (20 m).

BEHAVIOR
Occur singly or in small groups or aggregations.

FEEDING ECOLOGY AND DIET
Benthic carnivores that forage on the bottom for invertebrates, mainly crabs and shrimps, amphipods, polychaete worms, and gastropod mollusks.

REPRODUCTIVE BIOLOGY
Gonochoristic, with females tending to be larger than males. Courtship and spawning at night, with the release of pelagic eggs and larvae. Eggs are spherical and range in size from about 0.035 to 0.043 in (0.9–1.1 mm) in diameter. Hatching larvae are approximately 0.1–0.13 in (2.5–3.3 mm) in length, have unpigmented eyes, an unformed mouth, and a large yolk sac. Pigmentation develops with absorption of the yolk. The body is elongate but becomes deeper and compressed with growth, and silvery in color (paper-fish phase). The ventral keel also becomes prominent with growth. The gas bladder is small to moderate in size. The mouth becomes smaller and oblique with development. Larvae are adapted for a relatively long pelagic life.

CONSERVATION STATUS
Not listed by the IUCN. This species is rare in the Hawaiian Islands and may yet be proven distinct from those of the Southern Hemisphere populations.

SIGNIFICANCE TO HUMANS
Taken as a food fish, but smaller individuals may also be collected for the aquarium trade. ◆

Longnose hawkfish
Oxycirrhites typus

FAMILY
Cirrhitidae

TAXONOMY
Oxycirrhites typus Bleeker, 1857, Ambon Island, Moluccas, Indonesia.

OTHER COMMON NAMES
German: Gestreifter Schützenfish; Japanese: Kudagonbe.

PHYSICAL CHARACTERISTICS
Body slender, with an elongated snout; body whitish in color with a tartanlike pattern in red along body, snout, and dorsal fin; males larger than females within mating groups. To 5.1 in (13 cm).

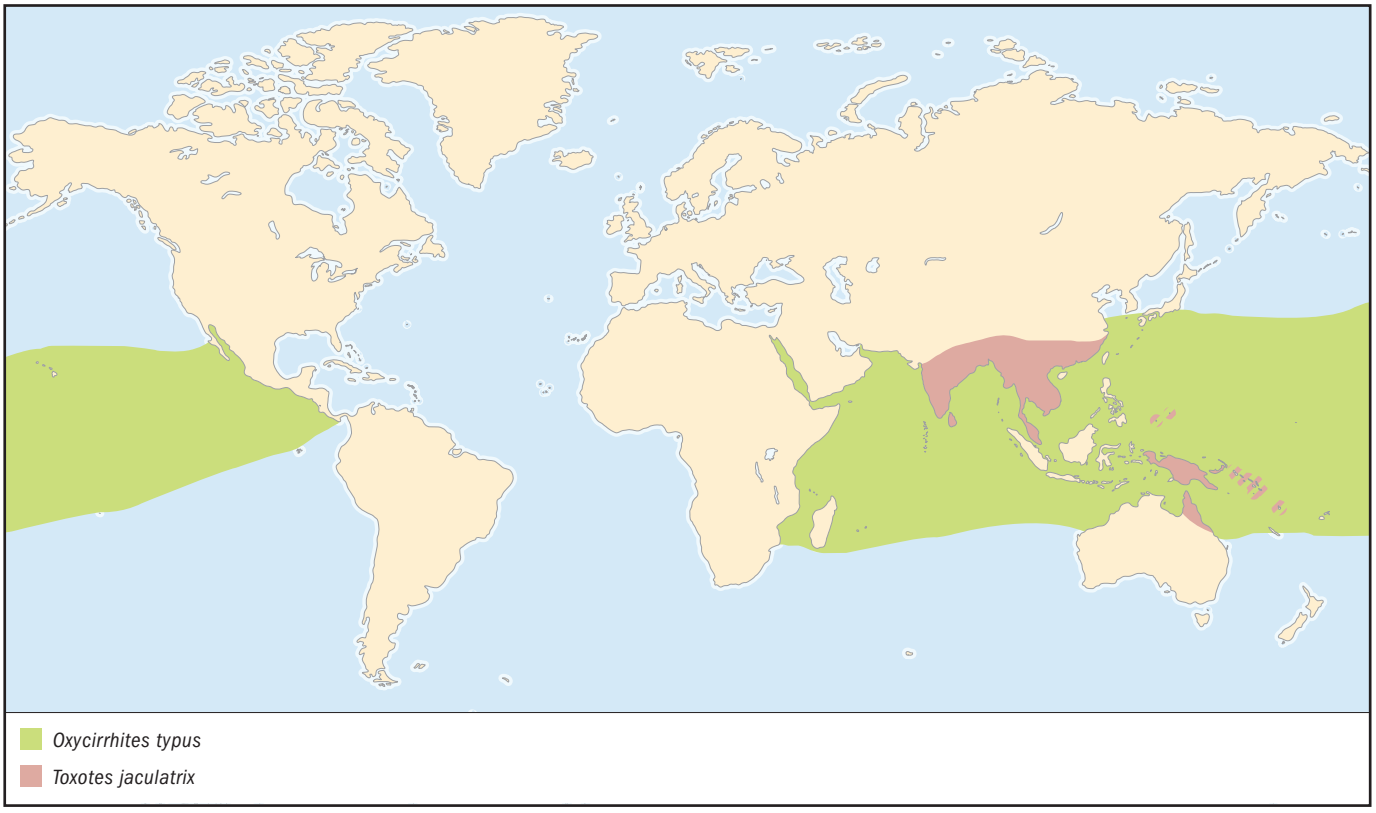
DISTRIBUTION
Red Sea east to Panama; southern Japan south to New Caledonia.

HABITAT
Usually deep slope or wall habitats in seaward coral or rocky reefs, passes, and lagoons; shallow rocky reefs in southern Baja California Sur, Baja Peninsula, Mexico, and occasionally found on shallow coral reefs elsewhere, particularly in areas of upwelling. Otherwise, more common in deeper reef habitats. Usually found in gorgonians (sea fans) and black corals.

BEHAVIOR
Occurs singly or in facultatively monogamous pairs on gorgonians and black corals. Will have a haremic mating system if the gorgonian or black coral is large or if others are close by.

FEEDING ECOLOGY AND DIET
Plucks small benthic and planktonic crustaceans with its long snout.

REPRODUCTIVE BIOLOGY
Protogynous hermaphrodites. Paired courtship and pelagic spawning just prior to or after sunset. If a male has a haremic mating group, he will move back and forth between females to court them until they spawn. Eggs and larvae are pelagic. Eggs are spherical, about 0.027 in (0.69 mm) in diameter, and hatch after 15 hours incubation at 80.6°F (27°C). The yolk sac is



large, and the jaws and eyes undeveloped. Pigmentation develops with absorption of the yolk. Larvae are elongate and compressed laterally. Possess a gas bladder that is lost in adults. Specializations for pelagic life include serrations on the preopercle, a chin barbel (which disappears with growth), and the presence of cirri on the spinous dorsal fin membrane and also on the anterior nostril.

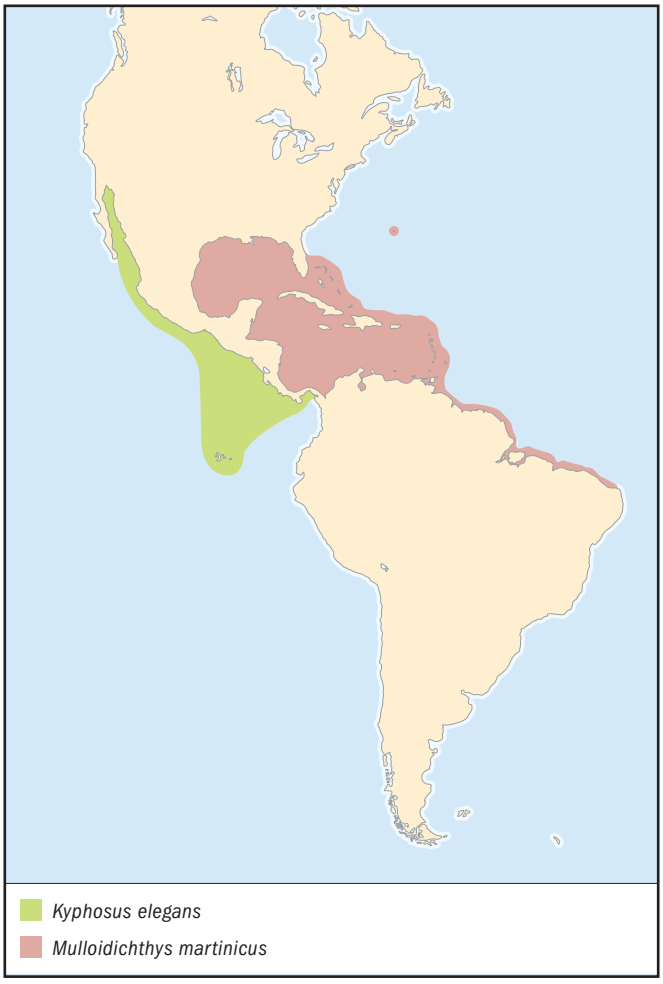
CONSERVATION STATUS
Not listed by the IUCN. Not commonly seen, despite its wide distribution, and population levels likely to be limited by available microhabitat. The collection of black corals for the jewelry trade and gorgonians for the ornamental trade poses a threat, as do unregulated harvests by the aquarium trade.

SIGNIFICANCE TO HUMANS
A highly prized aquarium species. ◆

Cortez chub
Kyphosus elegans

FAMILY
Kyphosidae

TAXONOMY
Kyphosus elegans Peters, 1869, Mazatlan, Sinaloa, Mexico.



OTHER COMMON NAMES
Spanish: Chopas.

PHYSICAL CHARACTERISTICS
Deep, compressed body with silver-gray color marked by faint brown stripes between scale rows on the flanks. Can quickly produce a pattern of white spots about the diameter of the eye. The jaw teeth are fixed and not freely movable. To 15 in (38 cm) total length.

DISTRIBUTION
Gulf of California south to Panama and west to the Galápagos Islands.

HABITAT
Rocky and coral reefs, usually in high-energy areas below the surf zone.

BEHAVIOR
Often found in large schools swimming in the water column.

FEEDING ECOLOGY AND DIET
Omnivorous but feeds mainly upon benthic algae.

REPRODUCTIVE BIOLOGY
The eggs are pelagic and about 0.039–0.043 in (1–1.1 mm) in diameter. Larvae hatch at 0.094–0.114 in (2.4–2.9 mm), are elongate, have a large yolk sac, unformed jaws, and unpigmented eyes. With growth, the head and mouth become large. Possesses a gas bladder. Head spines develop as a specialization for pelagic life.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be taken in subsistence fisheries or local commercial fisheries as a food fish. ◆

Mono
Monodactylus argenteus

FAMILY
Monodactylidae

TAXONOMY
Monodactylus argenteus Linnaeus, 1758, East Indies.

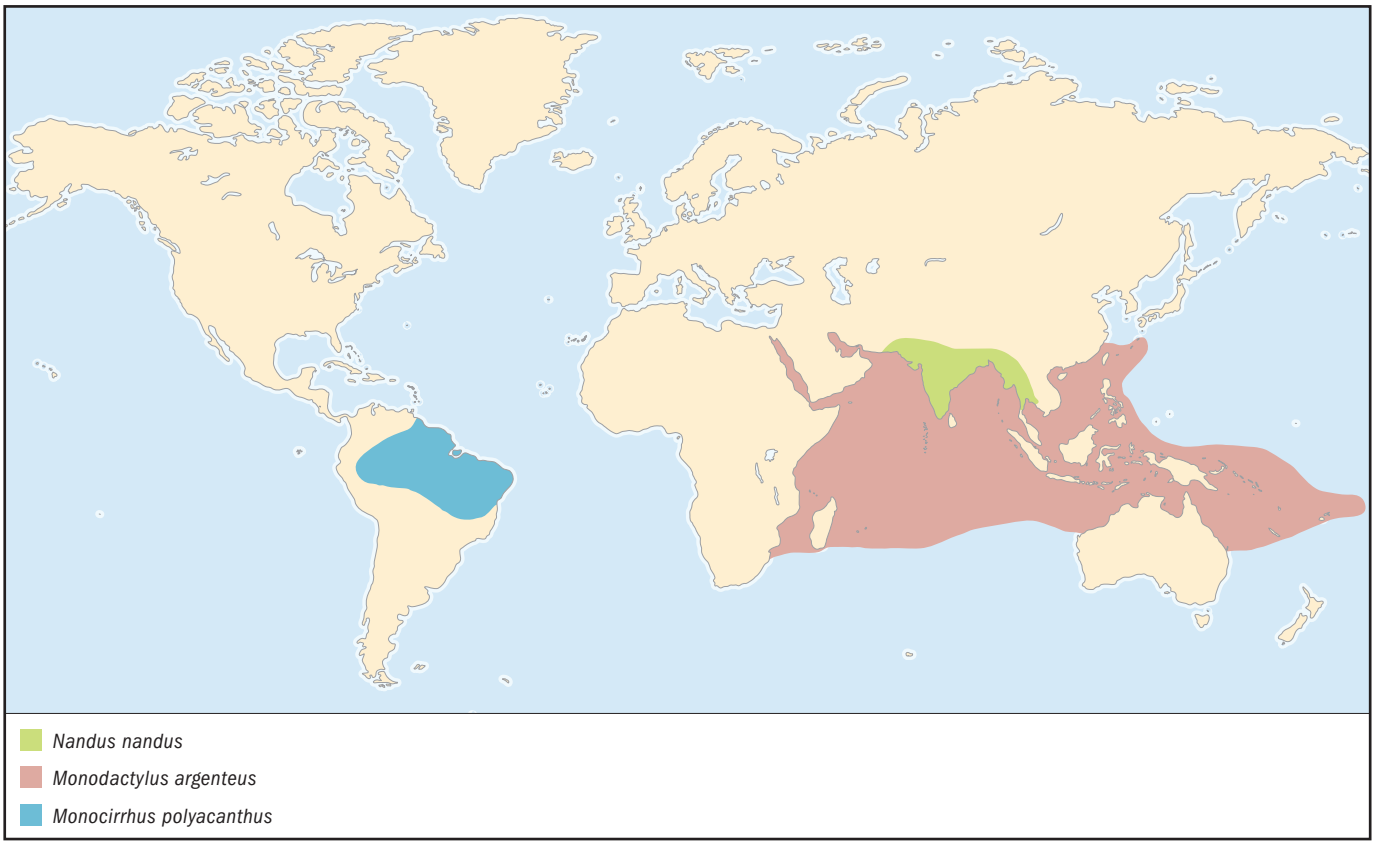
OTHER COMMON NAMES
English: Diamondfish, fingerfish, moony, silvery moony, Natal moony; Japanese: Himetsubameuo.

PHYSICAL CHARACTERISTICS
Deeply compressed body with silvery color marked by a slender dark-colored bar on the head. The anterior edges of the dorsal and anal fins are also dark colored, the fins are pale yellow. The pelvic fin is absent in adults. To 8.5 in (22 cm) total length.

DISTRIBUTION
Red Sea east to Samoa; Yaeyama Islands (southern Japan), south to Australia and New Caledonia.

HABITAT
Brackish waters, estuaries, and silty reefs.

BEHAVIOR
Found singly or in small groups among mangroves or other structures, but in large schools in estuaries and silty reefs where they swim in the water column.



FEEDING ECOLOGY AND DIET
Feed upon plankton in the water column and detritus on the bottom.

REPRODUCTIVE BIOLOGY
Spawns adhesive, demersal eggs in freshwater. Others in the genus spawn pelagic eggs in seawater. Eggs are spherical and approximately 0.039 in (1 mm) in diameter. The larvae hatch around 0.071 in (1.8 mm) in length, are compressed and moderate in depth, have a large yolk sac, an unformed mouth, and unpigmented eyes. With growth, the head becomes large with a convex dorsal profile that becomes steep over time. Possesses a small gas bladder. Larvae have pelvic fins that are reduced in adults. This character, plus the development of spines on the head, are viewed as specializations for pelagic life.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular as an aquarium fish. Maybe taken in subsistence fisheries as a food fish. ◆

Yellow goatfish
Mulloidichthys martinicus

FAMILY
Mullidae

TAXONOMY
Mulloidichthys martinicus Cuvier and Valenciennes, 1829, Martinique Island, West Indies.

OTHER COMMON NAMES
French: Poisson chèvre jaune.

PHYSICAL CHARACTERISTICS
Twin barbels on the lower jaw, a relatively short snout, the body elongate with two well-separated dorsal fins, two spines in the anal fin, and a forked caudal fin. There are 36–37 lateral line scales from the upper gill opening to the base of the caudal fin. These fishes are bronze and pale yellow in color with a yellow median stripe that extends along the length of the body, and grow to 12 in (30 cm) total length.

DISTRIBUTION
Western Atlantic, from Bermuda southwest to Florida and the Gulf of Mexico, and south from the Bahamas to Brazil.

HABITAT
Coral reefs and flats of sand or rubble.

BEHAVIOR
Swims lazily or hovers in schools above the bottom during the day and forages after dark.

FEEDING ECOLOGY AND DIET
Feeds by probing the bottom with its barbels in search of prey, usually at night or during low-light periods. The diet includes annelid worms, crabs, ophiurans, and to a lesser extent, small fishes.

REPRODUCTIVE BIOLOGY
Spawns in aggregations and produces pelagic eggs and larvae. Eggs are spherical and small, between 0.024–0.036 in (0.63–0.93 mm) in diameter. Larvae hatch between 0.063–0.134 in (1.6–3.4 mm) in length, are elongate, and have a large yolk sac, unformed jaws, and unpigmented eyes. Body pigmentation develops with absorption of the yolk sac. Possesses a gas bladder and a short

gut. The barbels form at about 0.67–0.71 in (17–18 mm) but remain recessed under the lower jaw. Post-larvae appear capable of a relatively long pelagic phase prior to settlement.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Highly esteemed as a food fish and taken in subsistence and local commercial fisheries. ◆

Amazon leaffish
Monocirrhus polyacanthus

FAMILY
Nandidae

TAXONOMY
Monocirrhus polyacanthus Heckel, 1840, Marabitanos, Brazil.

OTHER COMMON NAMES
English: Barbeled leaf fish, South American leaf-fish; German: Blattfisch; Spanish: Pez hoja.

PHYSICAL CHARACTERISTICS
Total length 3.9 in (10 cm). Body somewhat elongated, compressed, and basslike. Profile of forehead is steep and rises to the first dorsal spine at a point directly over the posterior edge of pelvic fin. A narrow, lurelike organ extends forward from the lower part of a protrusible mouth. Sharp dorsal, anal, and pelvic spines. Body color yellowish bronze to light or dark brown. Outer edges and tips of the anal, pelvic, and caudal fins are dark brown. Narrow dark brown stripe runs obliquely from a point midway up the forehead down through the eye, a second similar stripe runs obliquely from the lower operculum to the eye. A third, fainter band is found mid flank below the dorsal fin.

DISTRIBUTION
South America, from Guyana south to Brazil and west into the Peruvian Amazon.

HABITAT
Benthopelagic, primarily streams and rivers; often in association with or near submerged vegetation.

BEHAVIOR
Cryptic. Often found floating motionless, like a leaf, or in the cover of aquatic vegetation.

FEEDING ECOLOGY AND DIET
Carnivorous. An ambush predator that preys upon smaller fishes, and aquatic insects and their larvae. Engulfs prey rapidly by extending its large, protrusible mouth.

REPRODUCTIVE BIOLOGY
Gonochoristic. Demersal eggs are spawned and fertilized in a nest prepared by the male. Male parental care of eggs. Eggs hatch after three to four days and are free swimming by five days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected commercially for the aquarium trade. ◆

Gangetic leaffish
Nandus nandus

FAMILY
Nandidae

TAXONOMY
Nandus nandus Hamilton, 1822, Gangetic Provinces of India.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Typically basslike; pale olive-bronze color with loosely arranged vertical brownish olive bands along the flank and extending into dorsal fin. Noted for its sharp dorsal, pelvic, and anal spines.

DISTRIBUTION
From Pakistan east to Thailand.

HABITAT
Benthopelagic in freshwater ponds, ditches, flooded fields, lakes, reservoirs, canals, rivers, and estuaries.

BEHAVIOR
Often cryptic and holding to cover from where it can ambush prey.

FEEDING ECOLOGY AND DIET
Gangetic leaffishes are predators that feed upon smaller fishes and aquatic insects.

REPRODUCTIVE BIOLOGY
Gonochoristic. Males clean a spawning site, usually a rock or leaf, and then court the female, who spawns around 200–400 demersal eggs that are fertilized by the male. Male parental care has been observed in aquaria.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A prized food fish. Juveniles may also be taken for the aquarium trade. ◆

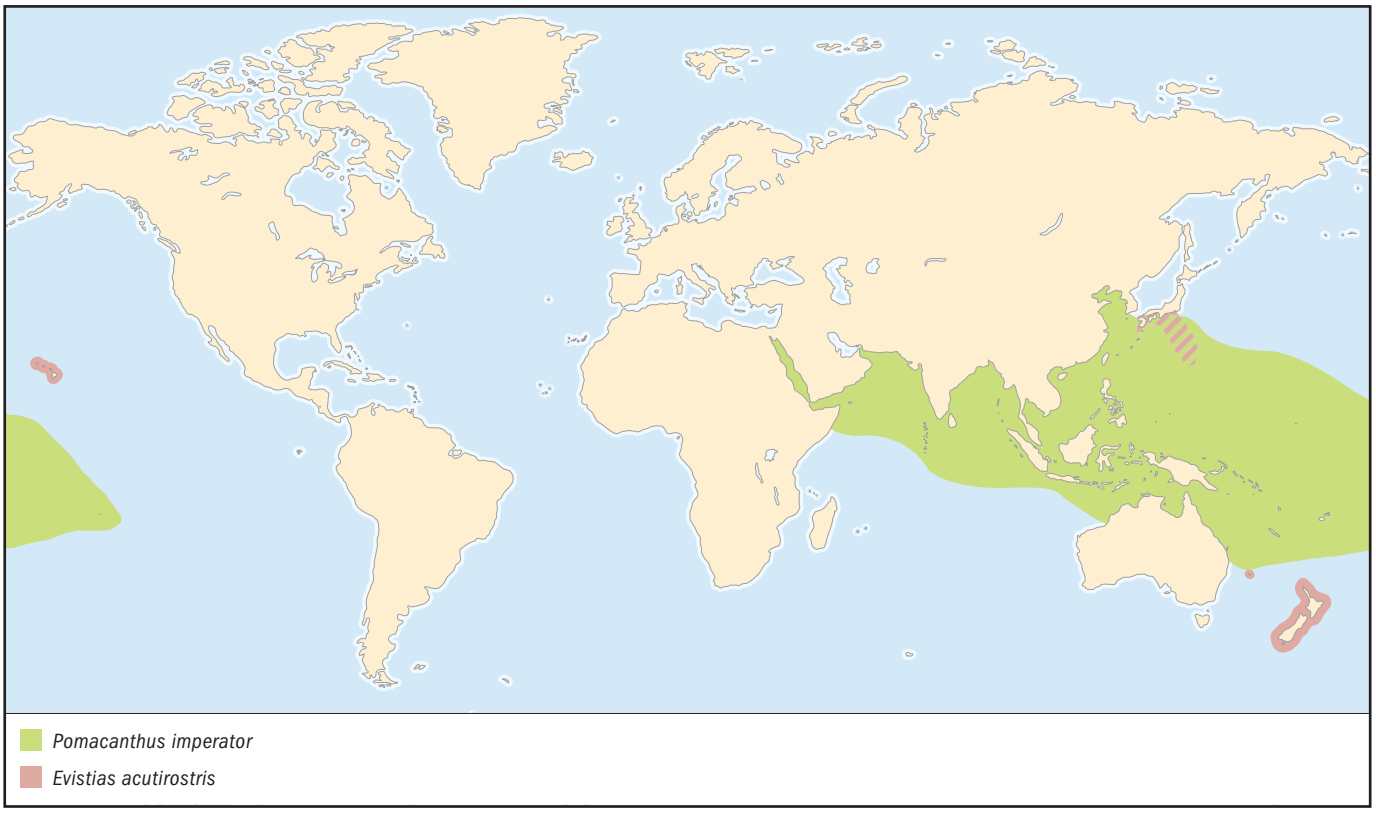
Striped boarfish
Evistias acutirostris

FAMILY
Pentacerotidae

TAXONOMY
Evistias acutirostris Temminck and Schlegel, 1844, Nagasaki, Japan.

OTHER COMMON NAMES
English: Whiskered armorhead; Japanese: Tenguidai.

PHYSICAL CHARACTERISTICS
Body deep with a sail-like dorsal fin; the lower jaw has many small barbels. Color pattern denoted by a dark brown face and alternating dark brown and white vertical bands along the



body; all fins are yellow except for the pelvic fins, which are dark brown. To 25.6 in (65 cm) total length.

DISTRIBUTION
Antitropical distribution, with populations in central and southern Japan, including the Izu and Ogasawara Islands, and Hawaii in the Northern Hemisphere and Lord Howe Island (Australia), and the islands of northern New Zealand in the Southern Hemisphere.

HABITAT
Generally a deep-slope fish, from 65 to almost 1,000 ft (20 to almost 330 m) deep, depending upon locality. Found among rocky and coral reefs, usually in or near caves.

BEHAVIOR
May be found in pairs or small groups.

FEEDING ECOLOGY AND DIET
Uses its snout and barbels to probe the bottom for various invertebrates.

REPRODUCTIVE BIOLOGY
Gonochoristic. Presumed to spawn pelagically, but little is known of its reproductive behavior and ecology. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN. Might be vulnerable because of its status as a commercial food fish.

SIGNIFICANCE TO HUMANS
Esteemed as a food fish, but juveniles and young adults are also taken, although infrequently, for the aquarium trade. ◆

Emperor angelfish
Pomacanthus imperator

FAMILY
Pomacanthidae

TAXONOMY
Pomacanthus imperator Bloch, 1787, Japan.

OTHER COMMON NAMES
Afrikaans: Keiser-engelvis; French (Polynesia): Poisson empereur; paraharaha; Japanese: Tatejima-kinchakudai.

PHYSICAL CHARACTERISTICS
Deeply compressed, with longish pelvic fins and a long preopercule spine. Adults and juveniles have distinct color phases. Adults are yellow with horizontal blue stripes along the flank, a deep purplish mask over the eye and on the flank above the pectoral fin, a white snout and mouth, and yellow fins with purplish blue stripes on the anal fin. Juveniles are deep navy blue to almost black, with concentric white circles on the flank and white bands on the head. One of the largest angelfishes, to over 15.7 in (40 cm) total length.

DISTRIBUTION
Red Sea east to the Line Islands and the Tuamotu Archipelago; southern Japan south to northern Australia, and southeast to Lord Howe Island and the Austral Islands. Reported from Hawaii, but either very rare as a stray or introduced from aquarium stock.

HABITAT
Coral reefs. Juveniles on patch reefs in lagoons, protected areas in lagoon passes, and among corals, in holes or under ledges

on outer reefs or reef flats; subadults move to surge channels and holes on reef fronts; and adults are found usually near caves and ledges of seaward reefs, passes, or lagoons.

BEHAVIOR
Usually observed paired or singly as they patrol a large home range; may display some intra- or interspecific territorial behavior (usually towards other similarly sized angelfishes). Have an haremic mating group, with subordinate females residing within the male's home range.

FEEDING ECOLOGY AND DIET
Feed almost exclusively on sponges and tunicates.

REPRODUCTIVE BIOLOGY
Protogynous hermaphrodites. Sequential courtship and spawning among members of a mating group occur at dusk. Eggs and larvae are pelagic. Eggs are round, approximately 0.023–0.039 in (0.6–1 mm) in diameter. Larvae hatch around 0.05–0.1 in (1.3–2.6 mm) in length, have a large yolk sac, an unformed mouth, and unpigmented eyes. With growth, they assume a deep, laterally compressed shape, and the profile of the head becomes steep. Possesses a gas bladder. The development of head spination and spinules (spine-like structures on the skin) are specializations for pelagic life.

CONSERVATION STATUS
Not listed by the IUCN. Because of apparent low population densities at many localities, this species is subject to overfishing by the aquarium trade.

SIGNIFICANCE TO HUMANS
Highly prized, especially the juveniles, as an aquarium fish. Adults are also taken occasionally in subsistence food fisheries. ◆

Banded archerfish

Toxotes jaculatrix

FAMILY
Toxotidae

TAXONOMY
Toxotes jaculatrix Pallas, 1767, Indian Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body is compressed and almost triangular, with a pointed head. Color is silvery white with five black bands across the upper sides of the body, the dorsal fin, and the caudal peduncle, and yellow on anal, caudal, and dorsal fins. These fishes grow to 8 in (20 cm) total length.

DISTRIBUTION
Widespread from India and Sri Lanka, east through Southeast Asia, the Ryukyu Islands, Palau and Yap in Micronesia, Melanesia, and parts of Queensland in northern Australia; also in Vanuatu.

HABITAT
Generally found in bays, estuaries, and the lower reaches of rivers and creeks, usually among mangrove branches and roots.

BEHAVIOR
Occurs singly or in small groups around shelter. Swims slowly as it hunts for prey both below and above the surface of the water. Will swim rapidly on occasion to challenge conspecifics. As with other archerfishes, the banded archerfish will hunt by shooting a stream of water drops at terrestrial prey above the surface.

REPRODUCTIVE BIOLOGY
Gonochoristic, with pair spawning and the release of demersal eggs near the bottom. Others in the genus release either pelagic or demersal eggs. Demersal eggs are larger compared to pelagic eggs in this species, about 0.023–0.031 in (0.6–0.8 mm) in diameter. Larvae hatch at 0.12 in (3 mm) in length, are pelagic, possess a large yolk sac, have an unformed mouth, and lack pigmented eyes. With growth, the body becomes moderate in depth and the mouth large. Possesses a gas bladder. The development of head spines is regarded as a specialization for pelagic life.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken in subsistence fisheries and as a light-tackle gamefish, but more importantly as an aquarium fish. ◆

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Organizations

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Terry J. Donaldson, PhD

Percoidei V

(Groupers, sea basses, trevallys, snappers, emperors, and relatives)

Class Actinopterygii
Order Perciformes
Suborder Percoidei
Number of families 29

Photo: Blue banded sea perches (*Lutjanus kasmira*) near Palau. (Photo by Animals Animals ©Joyce & Frank Burek. Reproduced by permission.)

Evolution and systematics

The suborder Percoidei contains more than 70 families and 2,800 species. This section on percoid fishes is widely divergent and includes the following 29 families: Ambassidae (glassfishes; Chandidae of some authors), Polyprionidae (wreckfishes), Serranidae (fairy basslets, groupers, hamlets, perchlets, sand perches, sea basses, soapfishes), Grammatidae (basslets), Callanthiidae (splendid perches), Pseudochromidae (dottybacks and eel blennies), Plesiopidae (longfins and roundheads), Glaucosomatidae (pearl perches), Opistognathidae (jawfishes), Priacanthidae (bigeyes), Apogonidae (cardinalfishes), Sillaginidae (sillagos or smelt whitings), Malacanthidae (tilefishes), Rachycentridae (cobias), Carangidae (jacks, pompanos, and trevallys), Menidae (moonfish), Leiognathidae (ponyfishes or slipmouths), Bramidae (pomfrets), Lutjanidae (snappers), Caesionidae (fusiliers), Lobotidae (tripletails), Gerreidae (mojarras), Haemulidae (grunts and sweetlips), Dinopercidae (cave basses or lampfishes), Sparidae (porgies), Lethrinidae (emperors), Nemipteridae (monocle or threadfin breams), Polynemidae (threadfins), and Sciaenidae (croakers and drums). As with other percoid fishes, these families date largely from the Lower Tertiary during the Eocene or Miocene. Fossil records from the Eocene have been discovered for the Serranidae, Pseudochromidae, Lutjanidae, Haemulidae, and Lethrinidae. The Priacanthidae dates from the Middle Eocene. The Apogonidae, Sillaginidae, Carangidae, Menidae, and Sparidae date from the Lower Eocene. The Malacanthidae and Sciaenidae date from the Miocene, and the Bramidae from the Upper Miocene. The Leiognathidae, however, dates from the Oligocene.

Diverse and speciose families include the Serranidae, with 62 genera and at least 449 species. This family is divided into three subfamilies, the Serraninae (sea basses), the Anthiinae (fairy basslets and perchlets), and the Epinephelinae, with the latter arranged into five tribes. These are the Niphonini (Japanese ara or grouper), Epinephelini (groupers and coral trouts), Liopropomini (Swissguard basslets), and the Diploprionini and Grammistini (both soapfishes). Other speciose families include the Apogonidae, with 22 genera and at least 207 species; the Carangidae, with 33 genera and 140 species; the Lutjanidae, with 17 genera and 103 species; the Haemulidae, with 17 genera and 150 species; the Sparidae, with 35 genera and 112 species; and the Sciaenidae, with 70 genera and at least 266 species.

Physical characteristics

Fishes of the family Ambassidae have perch-like bodies, a dorsal fin that is notched deeply, and a forked caudal fin. The bodies of many species are transparent or partially so. Body sizes range up to 10.2 in (26 cm) in total length, but most species are considerably smaller. The six species comprising the Polyprionidae are all large, robust grouper-like fishes with large heads and mouths, two rounded spines on the opercle, pelvic fins with one spine and 5 soft rays, and continuous lateral lines. Color patterns range from silvery to blue-gray to mottled. Body sizes range from 59 in (150 cm) to over 98 in (250 cm) in total length.

The Serranidae has considerable variation in morphology and body size. Most species have a single dorsal fin bearing spines and soft rays, small ctenoid scales, 2–3 flattened spines on the opercula, a continuous lateral line, a maxillary (upper jaw) that is exposed fully, and a lower jaw that extends beyond the maxillary. Members of the subfamily Anthiinae are rather small and quite colorful. Most water column-dwelling species have lunate caudal fins, while benthic-dwelling species tend towards caudal fins that are truncate. Males are often sexually di-

morphic; that is, they are distinguished in appearance from females with regard to body size, fin elongation, and color pattern. Groupers and soapfishes (tribe Epinephelini) are usually robust, bass-like fishes, although some soapfishes are elongate and slender. Most species have large heads and mouths, well-developed spines in the dorsal fin, and caudal fins that range from truncate to emarginate, lunate, or rounded. Swissguard basslets (tribe Liioproprionini) tend to be small and slender with flattened heads, and are often colorful. Soapfishes have dermal glands that secrete a toxin that is an effective antipredator mechanism. Groupers, soapfishes, and Swissguard basslets tend to be sexually dimorphic for body size, with males being larger than females. Adult body sizes range from less than 3.9 in (10 cm) to over 118 in (300 cm) in total length.

Species of the Grammatidae tend to be small and colorful. They have an interrupted lateral line, arranged in two segments; alternately, the lateral line is absent. There are 11–13 spines in the dorsal fin and one spine and five soft rays in the pelvic fin. Body sizes are usually less than 3.9 in (10 cm) in total length. The Callanthiidae is distinguished by having an compressed, oblong-shaped body, a single dorsal fin with 11 spines and 9–10 soft rays, an opercle with 1 or 2 spines, a lateral line running along the base of the dorsal fin, and truncate, emarginate, or excessively lunate caudal fins. Most have color patterns of bright orange, yellow, and red. Adults range in size from about 3.1 in (8 cm) to over 23.6 in (60 cm). Members of the Pseudochromidae follow one of two body plans. Those in the subfamily Pseudochrominae have somewhat elongate bodies; a long, continuous dorsal fin; small scales (cycloid anteriorly and ctenoid posteriorly); and many have rather brilliant color patterns. Some species lack a lateral line while others have one that is interrupted. Most species are less than 4.3 in (11 cm) in total length. Those in the subfamily Congrogadinae are eel-like in appearance and rather drably colored. Both dorsal and anal fins are long and continuous. They reach up to 20 in (50 cm) in total length. Species in the family Plesiopidae tend to be similar in shape to those in the Pseudochromidae, except that their bodies may be deeper in some genera. The dorsal fins have considerably more spines (11 to 14), too. The dorsal, anal, and caudal fins are large and exaggerated in the genera *Calloplesiops* and *Paraplesiops*. Most species are drably colored in comparison to the pseudochromids, but some species are remarkably colorful. Body sizes are usually less than 10 in (25 cm) in total length, many much smaller.

The Glaucosomatidae resembles deep-bodied serranids or haemulids. They have 8 spines and 12–14 soft rays in the dorsal fin and 3 spines and 12 soft rays in the anal fin. The maxilla is scaled, and the lateral line is straight and reaches the caudal fin. The caudal fin is either lunate or truncate. Color patterns tend to be dull gray or silver. Some have horizontal stripes that are black or yellow in color; one species, *Glaucosoma hebraicum* as a juvenile, has a distinctive black chevron stripe on the head and through the eye. Adults range from 15.7 in (40 cm) to over 47 in (120 cm) in total length. The Opistognathidae is recognized by having elongate, slender, or tapering bodies (although some are larger and robust), an enlarged head, large eyes, a continuous dorsal fin with 9 to 12 spines, pelvic fins placed ahead of the pectoral fins, and a lateral line that runs just under the dorsal fin and terminates halfway along the body. The scales are cycloid and the head is scaleless. Body sizes range up to 20 in (50 cm) in total length, but many species are much smaller. Members of the family Priacanthidae have deep, compressed bodies with very large eyes, a large, obliquely positioned mouth, a lower jaw that projects outward, rough scales, and scales on the head. Color patterns are usually red or coppery red and can be changed behaviorally to silver or mottled red and silver. Adults range in size to over 20 in (50 cm) in total length, but most species are less than 12 in (30 cm) long. Fishes of the family Apogonidae are generally small and compressed laterally, although some are elongate in shape. There are two dorsal fins, the first with 6–8 spines and the second comprised of soft rays. The anal fin has 2 spines. The mouth is relatively large and placed obliquely. The eyes are also large and adapted for low light conditions. Many species are colorful, but some are nearly transparent with faint shades of red, yellow, silver, or bronze. Adults range in size up to 10 in (25 cm) in total length, but the majority of species are considerably smaller.

The Sillaginidae is distinguished by having elongate bodies with two dorsal fins, the first bearing 10–13 spines and the second a single spine and 16–27 soft rays. The anal fin is elongate, with two spines and 14–26 soft rays. Color patterns tend to be silvery, white, or tan to match the color of the sea bottom. Fishes of the family Malacanthidae follow two body plans. Those in the genera *Hoplolatilus* and *Malacanthus* have relatively slender, elongate bodies with slightly rounded or pointed heads, truncate or somewhat-forked caudal fins, continuous dorsal fins, small scales that are largely ctenoid, and one spine or the opercle. *Hoplolatilus* species are often quite colorful, while *Malacanthus* tend to be striking despite coloration limited to black, white, some blue, or pale green. Tilefishes in the genera *Branchiostegus*, *Caulolatilus*, and *Lopholatilus* tend to be stockier, with larger, blunter heads. Colors range from pale or drab shades of brown, bronze, and green to pink. Body sizes range up to 49 in (125 cm) in total length. The single species of Rachycentridae, *Rachycentron canadum*, has an elongate body and depressed head. There are 6–9 short free spines positioned ahead of the long dorsal fin. There are 1–3 spines and 26–33 soft rays in the dorsal fin and 2–3 spines and 22–28 soft rays in the long anal fin. The caudal fin is lunate, with the lower lobe shorter than the upper. The body has a pattern of three darkly colored lateral stripes along the flank and, in juveniles and young adults, a long whitish silver stripe runs dorsally from the snout to the caudal peduncle. This species grows to over 79 in (200 cm) in total length.

The Carangidae is diverse in body form. Most species have deep, compressed bodies, two dorsal fins, forked caudal fins, and slender caudal peduncles bearing bony scutes. Some species are elongate and fusiform. Colors are typically silver or gray with ornamentation in black, blue, green, olive, or yellow. The pilotfish, *Naucrates ductor*, is bright yellow with black vertical stripes, however. Most species are less than 39 in (100 cm) in total length, but some will grow to over 98 in 250 cm). The Menidae has a disc-like body, a sharply angled, deep breast, and a nearly horizontal dorsal surface. The dorsal and anal fins are spineless but bear 43–45 and 30–33 soft rays, respectively. The first pelvic fin ray of adults is elongate, and the caudal fin is deeply forked. Color is blue dorsally and

Bar jacks (*Caranx ruber*) preying on herring near Bonaire Island in the Netherlands Antilles. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

white ventrally, with 2–3 rows of dark spots along the dorsal flank down to the lateral line. The Leiognathidae is distinguished by strongly compressed bodies; small cycloid scales; gill membranes that are unified at the isthmus; a continuous dorsal fin with 8–9 spines and 14–16 soft rays; an anal fin with 3 spines and 14 soft rays; and a forked caudal fin. These fishes also possess luminous organs on the throat and the ability to secrete mucus from their skin. Members of the Bramidae are deeply compressed with long, continuous dorsal and anal fins, long pectoral fins, and forked or widely forked caudal fins. Color patterns range from silver to bronze, dull red, or black. Members of the genus *Pteraclis*, the fan fishes, have excessively large dorsal and anal fins that give these fishes a fan-like shape. Adults range up to 39 in (100 cm) in total length, although most species are half of that size.

Species of the Lutjanidae have ovate or elongate bodies that are compressed moderately. The single dorsal fin is notched with 10 spines and 8–18 soft rays. The anal fin has 3 spines and 7–11 soft rays. The caudal fin is either truncate, emarginated, or forked deeply. Color patterns are highly variable. Most species are less than 39 in (100 cm) in total length, but some will grow to over 59 in (150 cm). The colorful Caesionidae is distinguished by slender and rather streamlined bodies, with small mouths and a protrusible upper jaw. There is a single dorsal fin with 9–15 spines and 9–21 soft rays. The anal fin has 3 spines and 9–13 soft rays. The caudal fin is forked deeply. Color patterns range from blue to silvery blue, with yellow, pink, or red accents. Most species are less than 23.6 in (60 cm) in total length. The single species of Lobotidae, *Lobotes surinamensis*, has an oval or oblong and compressed body, a single dorsal fin with 11–12 spines and 15–16 soft rays, an anal fin with 3 spines and 11–12 soft rays, and 17 soft rays in the pectoral fin. The dorsal, anal, and caudal fins are all rounded. The scales are ctenoid. Adults are dark brown or greenish yellow along the back, and silverfish gray along the flanks; juveniles tend to be brown and yellow, and are usually mottled. This species grows to about 39 in (100 cm) in total length.

Members of the Gerreidae are silvery in color, have moderately deep and compressed bodies, a head that is concave in profile ventrally, and protractile mouths. The scales are ctenoid and large, and the caudal fins are forked. Most species are less than 14 in (35 cm) in total length. The Haemulidae resembles the Lutjanidae in body shape, but a number of species tend to be more robust; have smaller mouths, thicker lips, and conical teeth; and lack canines. Their dorsal fins are continuous with 9–14 spines and 11–26 soft rays, and the anal fins are much shorter with 3 spines and 6–18 soft rays. The

caudal fins are truncate to slightly emarginate. Color patterns are variable. Most species are less than 23.6 in (60 cm) but some grow to at least 39 in (100 cm) in total length. The Dinopercidae is distinguished by an oval, compressed body, a protruding lower jaw, a continuous dorsal fin with 9–11 spines and 18–20 soft rays, an anal fin with 3 spines and 12–14 soft rays, and a truncate caudal fin. Scales are ctenoid and cover the body, head, and fins. Color patterns range from a dull blackish brown with white specks to a barred pattern of alternating dark and whitish colors. Size ranges of adults are from 12 in (30 cm) to over 30 in (75 cm) in total length. The diverse Sparidae is snapper-like in appearance, with compressed oblong or ovate bodies, a dingle dorsal fin with 10–13 spines and 8–15 soft rays, an anal fin with 3 spines and 8–14 soft rays, a forked or emarginate caudal fin, weakly ctenoid scales, scaly cheeks and opercula, and conical, incisiform or molar teeth. Color patterns are variable but often have a metallic sheen. Adult body sizes range from about 12 in (30 cm) to over 79 in (200 cm) in total length. The Lethrinidae resembles both the Lutjanidae and Haemulidae in appearance. There are 10 spines and 9–10 soft rays in the dorsal fin and 3 spines and 8–10 soft rays in the anal fin. The caudal fin is emarginate or forked. The lips are thick, the mouth terminal, and the front of the jaws support canine teeth while conical or molariform teeth are positioned along the side of the jaws. Color patterns are largely drab in most species, ranging from gray to silvery gray, olive, yellow, or brown. Some are distinctively black or yellow and have red, blue, black, yellow, or white markings or stripes. Adult body sizes range from about 12 in (30 cm) to over 39 in 100 cm) in total length.

Fishes of the family Nemipteridae have slender or ovate bodies, 10 spines and 9–10 soft rays in the dorsal fin, 3 spines and 7–8 soft rays in the anal fin, and forked caudal fins. Their eyes are relatively large. Color patterns are variable and often bright and distinctive. Body sizes of most adults are less than 14 in (35 cm) in total length. The very distinctive Polynemidae is distinguished by a blunt, rounded snout, elongate body, two dorsal fins, and a deeply forked caudal fin. The unusual pectoral fin has a detached lower portion consisting of 3–7 free rays that may be used to detect prey in turbid water. Color patterns tend to be, for the most part, drab shades of olive and silver. Adults can grow up to 71 in (180 cm) in total length. The highly diverse Sciaenidae has long notched dorsal fins, with 6–13 spines in the anterior portion and 1 spine and 20–35 soft rays in the anterior portion. There are 1–2 weak spines and 6–13 soft rays in the anal fin. The caudal fins are mainly emarginate or rounded. Color patterns vary from silvery white or gray to light brown, yellow, pale pink, or pale blue. Some species, such as those in the genus *Equetus*, are striking, however. Adult sizes range from less than 3.9 in (10 cm) to over 79 in (200 cm) in total length.

Distribution

The Ambassidae occurs in tropical and subtropical marine, brackish, and fresh waters of the Indo-West Pacific; freshwater species are especially prominent in Australia, India, and Southeast Asia. The Polyprionidae has a scattered distribution in temperate and subtropical waters of the Atlantic, Indian and Pacific Oceans. The Serranidae is distributed in tropical, subtropical, and temperate waters of the Atlantic, Pacific, and Indian Oceans; some species occur in freshwater. The Grammatidae is limited to tropical and subtropical waters of the western Atlantic and western Pacific Oceans. The Callanthiidae occurs in temperate, subtropical, and tropical waters of the eastern Atlantic, including the Mediterranean, and the Indian and Pacific Oceans. The Pseudochromidae occurs in tropical marine, rarely brackish, waters of the Indo-Pacific region. The Plesiopidae is found in tropical and subtropical waters of the Indian and Pacific Oceans. The Glaucosomatidae appears to be a continental family that ranges from Western Australia east to Japan. Both the Opistognathidae and the Priacanthidae occur in tropical and subtropical waters of the Atlantic, Indian, and Pacific Oceans. Fishes of the family Apogonidae are mainly marine in the tropical and subtropical Atlantic, Indian, and Pacific Oceans, but some species occur in fresh or brackish waters in the western Pacific. The Sillaginidae is distributed in tropical and warm temperate coastal and estuarine waters of the Indo-West Pacific, from Africa east to Australia and New Caledonia, and north to Japan. Most species are continental, and at least one species has entered the eastern Mediterranean via the Suez Canal. The Malacanthidae occurs largely in tropical and warm temperate waters of the Atlantic, Indian, and Pacific Oceans; one species occurs in brackish and marine waters of New Guinea, however. The Rachycentridae is found in marine and, to a lesser extent, brackish waters of the tropical, subtropical, and temperate continental waters of the Atlantic, Indian, and Pacific Oceans, and are absent from most insular localities on the Pacific Plate. The Carangidae is widely distributed in tropical, subtropical, and warmer temperate waters of the Atlantic, Indian, and Pacific Oceans; some species will enter brackish and coastal rivers. The Menidae is distributed in the Indo-West Pacific, but limited from the east coast of Africa east to Indonesia and Southeast Asia. The Leiognathidae is distributed in coastal waters of the Indo-West Pacific; one species has entered the Mediterranean Sea via the Suez Canal, however. The Bramidae occurs in deeper oceanic waters of the tropical and temperate Atlantic, Indian, and Pacific Oceans. The Lutjanidae is found mainly in tropical and subtropical waters of the Atlantic, Indian, and Pacific Oceans, but some species also enter brackish and freshwater reaches; at least one species has been introduced successfully into freshwater lakes in Australia. The Caesionidae is distributed in tropical and subtropical waters of the Indo-West Pacific. The Lobotidae occurs in pelagic and coastal waters of the tropical Atlantic, Indian, and Pacific Oceans. The Gerreidae is found in coastal tropical and subtropical marine and, to a lesser extent, brackish waters of the Atlantic, Indian, and Pacific Oceans. Most species in the family Haemulidae occur in tropical and subtropical regions of these oceans as well, but some species also occur in brackish and coastal fresh waters. The Dinopercidae is restricted to warm temperate and subtropical localities of the western Indian Ocean and in the southeastern Atlantic off the coast of southern Africa from Angola to South Africa. The Sparidae is distributed largely in continental marine waters of the tropical and temperate Atlantic, Indian, and Pacific Oceans, but is also rare in fresh and

brackish water. With one exception, the Lethrinidae is limited to tropical and subtropical waters of the Indian and Pacific Oceans. A single species occurs off West Africa in the Atlantic Ocean. The Nemipteridae is found in the tropical and subtropical Indo-West Pacific. The Polynemidae is found in tropical and warm temperate marine, brackish, and freshwaters of the Atlantic (including the Mediterranean Sea), Pacific, and Indian Oceans. The Sciaenidae occurs in tropical, subtropical, and temperate waters. Most species are found in marine or brackish waters of the Atlantic, Indian, and Pacific Oceans, but some occur in freshwater drainages with current or historical connections to the sea.

Habitat

The Ambassidae occurs in coastal marine, brackish, and fresh waters, mainly in protected areas with overhanging or emergent vegetation, such as mangroves; swamps, ponds, ditches, billabongs, creeks, and deep holes in rivers are among the freshwater habitats where these fishes may be found. The Polyprionidae frequents deep slope rocky reefs and pinnacles, rock bottoms, or sand flats and kelp beds at depths of 16–1,968 ft (5–600 m), or more, depending upon the species. These fishes also associate with shipwrecks, and at least one species has been found inhabiting structure around a deep water thermal vent system.

The Serranidae, owing to its great diversity, frequents a wide variety of habitats in tropical and temperate marine, brackish, and freshwaters. Many species are found on seaward or protected coral or rocky reefs, often hiding in caves, holes, and crevices, under corals and ledges. Some species hover above some form of structure or swim actively in the water column. Some frequent sand, mud, rubble, mangrove, sea grass, or algal flats in estuaries and rivers, as well as on reefs. Others, such as most fairy basslets (subfamily Anthiinae), hover over deep slopes or pinnacles on reefs. Soapfishes (tribe Grammistini) and Swissguard basslets (tribe Liopropomini) are often associated with caves, crevices, or holes. Depth ranges vary, depending upon the species, from one to over hundreds of meters.

The Grammatidae lives in close association with structure, mainly holes and corals on coral reefs at depths down to over 1,198 ft (365 m); most species are found below 98 ft (30 m). The Callanthiidae prefers coral and rocky reef habitats at depths usually greater than 66 ft (20 m). The Pseudochromidae is often associated with structure on coral reefs, usually in holes, tubes, or caves, under rocks and corals, or in crevices, but some species may also be found on rubble flats. One species of eel-blenny (subfamily Congrogadinae) lives among sea urchin spines. Depth ranges vary from one to over 180 ft (55 m). The Plesiopidae is also found among holes, under rocks, and in caves but, these fish emerge at night to move along the bottom. The Glaucosomatidae occurs on deeper offshore rocky reefs, hard flat bottoms in deeper water, and possibly coral reefs as well. Depth ranges are 33 ft (10 m) to well over 656 ft (200 m). The Opistognathidae excavates burrows in sand and gravel on coastal reefs and flats.

The Priacanthidae dwells among rocks or corals on seaward coral and rocky reefs, occasionally on deeper flats, at depths of a few to over 656 ft (200 m). The highly diverse Apogonidae utilizes an equally diverse array of habitats. A number of species associate with structure, usually branching or eroded corals and rocks, on coral and rocky reefs. Others frequent holes, caves, crevices, ledges, rubble, silty or sandy bottoms, algal beds, sea grasses, mangroves, sponges, and even sea urchin and crown-of-thorns starfish spines. Still others occur in estuaries, rivers, creeks, ponds, and lakes, usually in association with structure. Depending upon the species and habitat, depths range from 3 ft (1 m) to over 262 ft (80 m). The Sillaginidae is found in shallow coastal waters, usually over sand or mud flats, and often along beaches; some species enter estuaries. The Malacanthidae may be found on coral and rocky reefs, deep sand and rubble flats, and, at least for one species, in shallow brackish water habitats. Depths range from 33 ft (10 m) to 1,640 ft (500 m), but most species occur in less than 656 ft (200 m) of water. The Rachycentridae swims in the pelagic water column but is also associated with structure, such as oil or sulfur drilling platforms, offshore piers, and drifting logs. The Carangidae is associated with a variety of coral and rocky reef habitats that range from sand, rubble, mud, algal and sea grass flats, boulder fields and old lava flows, and the water column inshore and in the open ocean. Some species enter estuaries and rivers or brackish water ponds. Depth ranges vary from 3 ft (1 m) to over 656 ft (200 m). The Menidae is found on inshore sand and mud flats, off deeper coral reefs, or in estuaries. The Leiognathidae frequents inshore sand and mud flats; some species enter freshwater. The Bramidae is pelagic, dwelling on deep-slopes and shelves, and is usually found at depths of over 656 ft (200 m).

The Lutjanidae is found mainly on seaward or protected coral and rocky reefs, usually in association with coral formations and rocks, but also hovering in the water column. Other species frequent sea grass, algal, rubble, and sand flats. A few species occur in estuaries, and one species ranges from marine to freshwaters, where it shelters in mangroves or similar kinds of emergent vegetation. Deep water species are associated with pinnacles. Depth ranges are from 3 ft (1 m) to over 1,476 ft (450 m). The Caesionidae swims in the water column over coral reefs, especially along outer slopes and lagoon pinnacles. The Lobotidae occurs in two widely divergent habitats. Juveniles and smaller adults may be found in the open sea, often around floating vegetation, flotsam, and jetsam. Alternately, these fishes may also be found on inshore flats and estuaries. The Gerreidae frequents inshore sand and mud flats, and may enter brackish or freshwater on occasion. The Haemulidae may be found on coral and rocky reefs, where they shelter near or under ledges. Some species are also found in brackish and freshwater. Members of the Dinopercidae are found in association with rocky and coral reefs, usually in caves or under ledges, to a depth of about 164 ft (50 m); juveniles may be found around rocky shorelines. The Sparidae is found on coral and rocky reefs, rubble and sand flats, or, rarely, in brackish and freshwater habitats. The Lethrinidae and the Nemipteridae also frequent coral and rocky reefs, as well as rubble, sand, and sea grass flats. The Polynemidae can be found on mud and sand flats in marine and brackish water, although some species also occur in similar habitats in rivers. The Sciaenidae inhabits a variety of habitats including mud, sand, and rubble flats and beaches,

shell reefs, coral and rocky reefs, and flooded salt marshes. Some species may also be found in freshwater rivers and lakes. Depth ranges vary from 3 ft (1 m) to over 328 ft (100 m).

Feeding ecology and diet

The Ambassidae preys upon benthic invertebrates; freshwater species will also feed upon aquatic and terrestrial insects, and algae. Feeding activity occurs during the night and, to a lesser extent, during the day. Predators include larger fishes, wading and diving birds, and, in freshwater habitats, reptiles. The Polyprionidae feeds upon benthic fishes, cephalopods, and large crustaceans. Predators are likely larger fishes that feed upon juveniles, but some toothed whales, including sperm whales, prey upon adults. Many members of the Serranidae are predators upon smaller fishes, crustaceans, and cephalopods. Others, particularly members of the subfamily Anthiinae, are planktivores that feed upon zooplankton in the water column. Larger fishes, including sharks and even other serranids, are predators upon these fishes. With the exception of the anthiines, most predation likely takes place upon juveniles, however. The Callanthiidae feeds upon zooplankton, mainly crustaceans. Predators of juveniles and adults include larger fishes that forage in the water column during daylight. The Pseudochromidae and Plesiopidae feed upon benthic invertebrates and small fishes. They likely fall prey to benthic ambush predators such as groupers and scorpionfishes. The Glaucosomatidae feeds upon smaller fishes, crustaceans, and cephalopods. Members of this family may be preyed upon by larger fishes; juveniles are likely to be more susceptible. The Opistognathidae feeds upon benthic invertebrates but also plucks zooplankton out of the water column. Predators of adults likely include ambush predators such as groupers, and possibly moray eels and sea snakes that investigate their burrows.

Fishes of the family Priacanthidae are nocturnal predators that feed upon both invertebrates and smaller fishes. In turn, they likely fall prey to larger predatory fishes. The Apogonidae feeds mainly upon zooplankton or benthic invertebrates, usually at night, but members of the genus *Cheilodipterus* are predatory upon smaller fishes as well. Predators of apogonids are usually larger ambush and foraging fishes such as groupers, scorpionfishes, and trevallys. Members of the Sillaginidae feed upon benthic invertebrates that they take from sand or other soft sediments. Predators include larger roving predatory fishes. The Malacanthidae feeds upon benthic invertebrates or zooplankton. Members of this family are likely preyed upon by larger fishes, especially when young. The Rachycentridae feeds upon smaller fishes, cephalopods, and crustaceans in the water column or around structure. Juveniles are probably more susceptible to predation from other pelagic fishes than adults, although sharks might prey upon the latter. Most members of the Carangidae are swift-moving predators of smaller fishes, crustaceans, and cephalopods. Some species feed exclusively in the pelagic realm, while most others feed on benthic or epibenthic prey. Members of the genus *Decapterus* strain zooplankton from the water column. Juvenile *Scomberoides* feed on the scales of inshore fishes such as mullets (Mugiloididae). The pilotfish, *Naucrates ductor*, accompanies sharks and feeds upon scraps leftover by these predators. This, and some other species in this family, will also swim alongside rays while foraging opportunistically for prey disturbed by the rays' movements. Carangids, especially juveniles and smaller species, are preyed upon by larger fishes and may also fall prey to some dolphins or other smaller toothed-whales.

Both the Menidae and Leiognathidae forage upon benthic invertebrates, although members of the latter family may also feed upon larger zooplankton in the water column at night. They may be preyed upon by larger fishes, such as sharks and mackerels. The Bramidae feeds upon small fishes, large planktonic crustaceans, and cephalopods in the water column. Larger pelagic fishes likely prey upon them in return. Most species of Lutjanidae are predatory upon smaller fishes, crustaceans, mollusks, or worms. A number are planktivores, however. Members of this family are susceptible to predation by larger fishes, especially when juveniles or young adults. The Caesionidae feeds in schools or aggregations upon zooplankton in the water column. Larger pelagic or epibenthic fishes are their predators. The Lobotidae feeds upon benthic crustaceans and small fishes inshore or near floating objects and *Sargassum* patches in the open sea. Members of this family often float sideways to mimic plant life, such as leaves or fronds, and then ambush their prey. Juveniles are probably more susceptible to predation than adults, although the latter may be preyed upon when drifting near the surface by pelagic predators. Members of the Gerreidae use their protrusible mouths to root out, sort, and feed upon benthic invertebrates from sand or other soft sediments. They are preyed upon by larger roving or ambush predatory fishes. Members of the family Haemulidae are accomplished at feeding upon hard-shelled benthic invertebrates such as mollusks and crustaceans, but some species also feed upon smaller fishes and benthic worms. Juveniles are likely to be more susceptible to predation than adults in the larger species; otherwise, larger fishes are their chief predators. The Dinopercidae also feeds upon benthic invertebrates and possibly smaller fishes. Their predators are doubtless larger fishes, and juveniles are more likely to be preyed upon than adults. The Sparidae usually feeds upon hard-shelled benthic invertebrates (mollusks and crustaceans). Their main predators are probably larger fishes.

The Lethrinidae usually feeds at night upon smaller fishes and benthic invertebrates that range from crustaceans and mollusks to polychaete worms, tunicates, and starfishes and their relatives. Larger fishes, including roving and ambush predators, are their likely predators, and juveniles are probably more susceptible to predation than adults. The Nemipteridae also has a variable diet, for these fishes feed upon crustaceans, polychaete worms, cephalopods, or small fishes; some species feed upon zooplankton. Members of this family are preyed upon by larger fishes. The Polynemidae sifts through soft sediments with elongated pelvic fin rays in search of benthic invertebrates and small fishes. Larger fishes such as sharks, and, depending upon the locality, large carnivorous reptiles such as estuarine crocodiles likely prey upon these fishes. Juveniles probably fall prey to ambush or roving predatory fishes such as flatheads (Platycephalidae) and trevallys (Carangidae). The Sciaenidae consists of benthic

predators of small fishes, crustaceans, and other benthic invertebrates. Their predators range from larger fishes to wading birds.

Behavior

The Ambassidae gathers in aggregations, some times quite large, under shelter. At night, these fishes become active and disperse as they feed. Fishes of the family Polyprionidae are probably territorial and patrol rather large home ranges. Within the Serranidae, the subfamilies Serraninae and Epinephelinae are largely solitary and territorial. Species that form haremic mating systems have multiple territories within that of a single male. Most species make good use of shelter or the bottom, from where they can avoid predation and also ambush prey. Some species are active swimmers in the water column, however. Many fairy basslet species (Anthiinae) aggregate in the water column but seek shelter on the bottom or against the faces of steep reef slopes, while others move, often cryptically, along the bottom. Males are territorial. Soapfishes (Diploprionini and Grammistini) and Swissguard basslets (Liopropomini) hover or rest in caves and holes, although some species move freely through the water column just above the bottom. These fishes seem to be more active at night. The Callanthiidae hovers in the water column singly or in groups, but the Grammatidae, Pseudochromidae, and Plesiopidae all tend to hide in holes, under rocks or corals, or in some other form of shelter, where they wait to ambush prey. Many colorful pseudochromids hover outside of their shelters, however. The Plesiopidae forages outside of shelter at night as well. Fishes in these families tend to be territorial. The behavior of the Glaucosomatidae is not well known. Members of this family shelter in caves or holes when approached and are likely to patrol a territory or home range. Adults and juveniles tend to move to shallower waters seasonally during cooler months. Jawfishes (Opistognathidae) excavate burrows with their large mouths and use them for shelter and nesting sites. When not in a burrow, they may be seen hovering above it in the water column; they enter the burrow tail first.

The Priacanthidae and the Apogonidae generally associate with structure during daylight but move into the water column to forage at night. Their relatively large eyes are used to detect both prey and predators. The Sillaginidae forages singly or in aggregations on sand or mud bottoms. The Malacanthidae lives singly, in pairs, or in haremic social groups and excavates burrows in the sand, where these fishes live when they are not hovering in the water column. Some of these burrows are distinguished by rather large mounds of rubble. The Rachycentridae is active in open water but will associate with structure. The Carangidae moves singly, in pairs or small aggregations, or in large schools either along the bottom or up in the water column. The Menidae forages in schools. The Leiognathidae forms schools and forages over the bottom during daylight; at night, these fishes move into the water column and may communicate with one another (directly or indirectly) by light flashes generated by bioluminescent organs on their throats.

Little is known about the behavior of the Bramidae because of the depths in which they live. Presumably, they form aggregations or schools that move up and down in the water column during night and day, respectively, as they follow their prey. The Lutjanidae hides under shelter, hovers in the water column, or forms aggregations that move lazily over the bottom. Some species are territorial and others patrol home ranges. The Caesionidae forms aggregations or schools that swim actively in the water column. A number of species appear to be able to change their color patterns behaviorally. Lobotidae juveniles and young adults often swim on their sides and hover under floating vegetation or logs, and may mimic leaves as well. Adults tend to be solitary. The Gerreidae forms small or large aggregations and forages actively along the bottom. The Haemulidae, depending upon the species, occurs singly or forms small or large aggregations. Members of this family seek shelter under ledges or in large holes during daylight but forage after dark. Alternately, they may form aggregations that swim lazily along the reef. Some aggregating species make daily migrations at dawn and dusk, and knowledge of the paths of these migration routes is transmitted culturally within social groups. The Dinopercidae shelters during daylight but likely moves about after dark. Members of this family can make a drumming sound by contracting muscles; the sound of the contraction is amplified by the swim bladder. The Lethrinidae moves singly, in small aggregations, or in large schools along the bottom; some species swim or hover up in the water column. The Nemipteridae either swims singly or in aggregations well up in the water column, rather like the Caesionidae, or these fishes dart about or hover alone or in groups just above the bottom. The Polynemidae swims just above the bottom, and these fishes use their specialized pelvic fins to detect prey as they forage. Their behavior is not well known. The Sciaenidae occurs singly or in groups, sometimes large aggregations, and members of the family swim actively along the bottom as they search for prey. As with the Dinopercidae, these fishes can communicate by the production of drumming sounds. Their hearing is well developed, too, which is useful for detecting prey, predators, and conspecifics (other members of the same species).

Reproductive biology

The Ambassidae spawns demersal eggs that are scattered on vegetation in freshwater; in marine and brackish waters, these fishes appear to spawn pelagic eggs. The larvae are pelagic, although those of freshwater species hold close to shelter. Some species of the Polyprionidae reportedly aggregate to spawn during summer months. Their eggs and larvae are pelagic. Details about deep-dwelling species are largely unknown, but it is assumed that they have a similar life history pattern. The reproductive behavior and ecology of the Serranidae is complex owing to the diversity of taxa within this family. Serranine fishes are hermaphroditic, but unlike other serranids this hermaphroditism is simultaneous rather than sequential. Thus, mature fishes can produce both eggs and sperm simultaneously. Courtship in these fishes may involve considerable ritual, as in the hamlets (*Hypoplectrus*), or virtually none at all, as in the genus *Serranus*. In the latter case, it has been hypothesized that a rapid spawning ascent without much visible courtship is a mechanism that prevents rivals from parasitizing spawning events by sneaking or streak-

ing during the spawning rush. Sometimes, however, triad or group spawning occurs. Eggs and larvae of these fishes are probably pelagic. Anthiine fishes include protogynous hermaphrodites, small single-male or larger multi-male haremic mating systems, pelagic spawning, and pelagic eggs and larvae. Courtship and spawning begin around sunset. Spawning is seasonal at higher latitudes but may spawn nightly at low latitudes. Epinepheline fishes include protogynous hermaphrodites (sex change from male to female) and secondary gonochorists (primary males within the same species). Mating systems may be haremic (e.g., in the genus *Cephalopholis* or in smaller *Epinephelus* species) or in pairs or groups within spawning aggregations (e.g., larger *Epinephelus* or *Plectropomus* species). At low population densities, some aggregating species appear to have haremic mating systems. Courtship usually commences prior to sunset with spawning after sunset and into darkness. Spawning, eggs, and larvae are pelagic. Little is known about the reproductive biology of soapfishes (tribes Diploprionini and Grammistini) and Swissguard basslets (tribe Liopropomini). They may be either protogynous hermaphrodites or secondary gonochorists (derived from hermaphroditic ancestors). Mating systems may be monogamous or haremic. Spawning is presumed to be pelagic, as are the eggs and larvae.

Little is known about the reproductive behavior of the Callanthiidae. Eggs and larvae are pelagic, however. Members of the Pseudochromidae are demersal spawning fishes. Females lay a ball of eggs that are fertilized and then guarded by males; alternately, some species are mouthbrooders. The Plesiopidae spawns demersal eggs on the undersides of rocks; alternately, they are mouthbrooders. Eggs are bound together into a small mass by chorionic filaments. The Glaucosomatidae do not change sex. Although the details of this family's reproductive biology are not well known, courtship and spawning are pelagic and eggs are broadcast over the bottom. Larvae are pelagic. In western Australia, one species spawns through the summer. The Opistognathidae practices mouthbrooding and cares for a ball or small mass of eggs that is tightly bound together by chorionic filaments. Although the details of courtship and spawning are largely unknown, the Priacanthidae may spawn in aggregations and produce pelagic eggs and larvae. Most species of Apogonidae are mouthbrooders. Eggs are spherical or spindle-shaped and range in size depending upon the species, and the larvae disperse (albeit poorly in a number of species) pelagically. The larvae of one species, the Banggai cardinalfish, *Pterapogon kauderni*, do not disperse; this life history trait explains this species' limited geographical distribution.

The Sillaginidae spawns pelagically, producing pelagic eggs and larvae; some species have been cultured artificially. The Malacanthidae has a mating system of either monogamy or haremic polygyny (one male and multiple females). Spawning is pelagic, as are the eggs and larvae. Little is known of the reproductive biology of the Rachycentridae. Spawning is presumed to be pelagic. Spawning aggregations have been reported for some species of Carangidae, and this trait may likely be true throughout the family. Eggs and larvae are pelagic. The spawning mode of the Menidae is unknown but is presumed to produce pelagic eggs and larvae. Details about spawning behavior of the Leiognathidae are also few, but pelagic eggs and larvae are produced. Little is known about reproduction in the Bramidae. Presumably, members of the family have pelagic eggs and larvae. Spawning aggregations have also been reported for the Lutjanidae and the Caesionidae. Courtship and spawning usually takes place near dusk. Some species reportedly do this in groups that split off from the main aggregation and spawn in the water column. Eggs and larvae are pelagic. The reproductive biology of the Lobotidae is not well known, but it is assumed that spawning, eggs, and larvae are all pelagic. The Gerreidae spawns either pelagically or by scattering eggs over the bottom. Some species form spawning aggregations over sand late in the afternoon during periods around the full moon. Their larvae are pelagic. Some Haemulidae have been observed forming spawning aggregations around the new moon in late spring. Spawning, eggs, and larvae are also pelagic. The Dinopercidae likely also spawn pelagically; little is known of their reproductive biology.

The reproductive biology of the Sparidae is complex. Many species are hermaphroditic, changing from one sex to the other with growth, while others are simultaneously so. Most species spawn pelagic eggs but some deposit demersal eggs in nests. The larvae are pelagic. The Lethrinidae include a number of species that are protogynous hermaphrodites. Spawning aggregations have been reported for some species, with courtship commencing after sunset. Spawning for many species occurs at peaks around the new moon and also seasonally. Spawning is pelagic, as are the eggs and larvae. Protogynous hermaphroditism has also been reported for the Nemipteridae. Spawning, eggs, and larvae are also pelagic. The reproductive biology of the Polynemidae is largely unknown. These fishes appear to be pelagic spawners; their eggs and larvae are pelagic. Although considerable effort has been devoted to the study of the eggs and larvae of the Sciaenidae (mainly for aquaculture purposes), surprisingly little is known about their reproduction in nature. A number of species are known to form spawning aggregations during summer and well into late autumn at lower latitudes. Males often produce drumming noises during courtship of females. Spawning is known to be pelagic for these species, as are their eggs and larvae, but other species have larvae, and perhaps eggs and spawning, that are demersal.

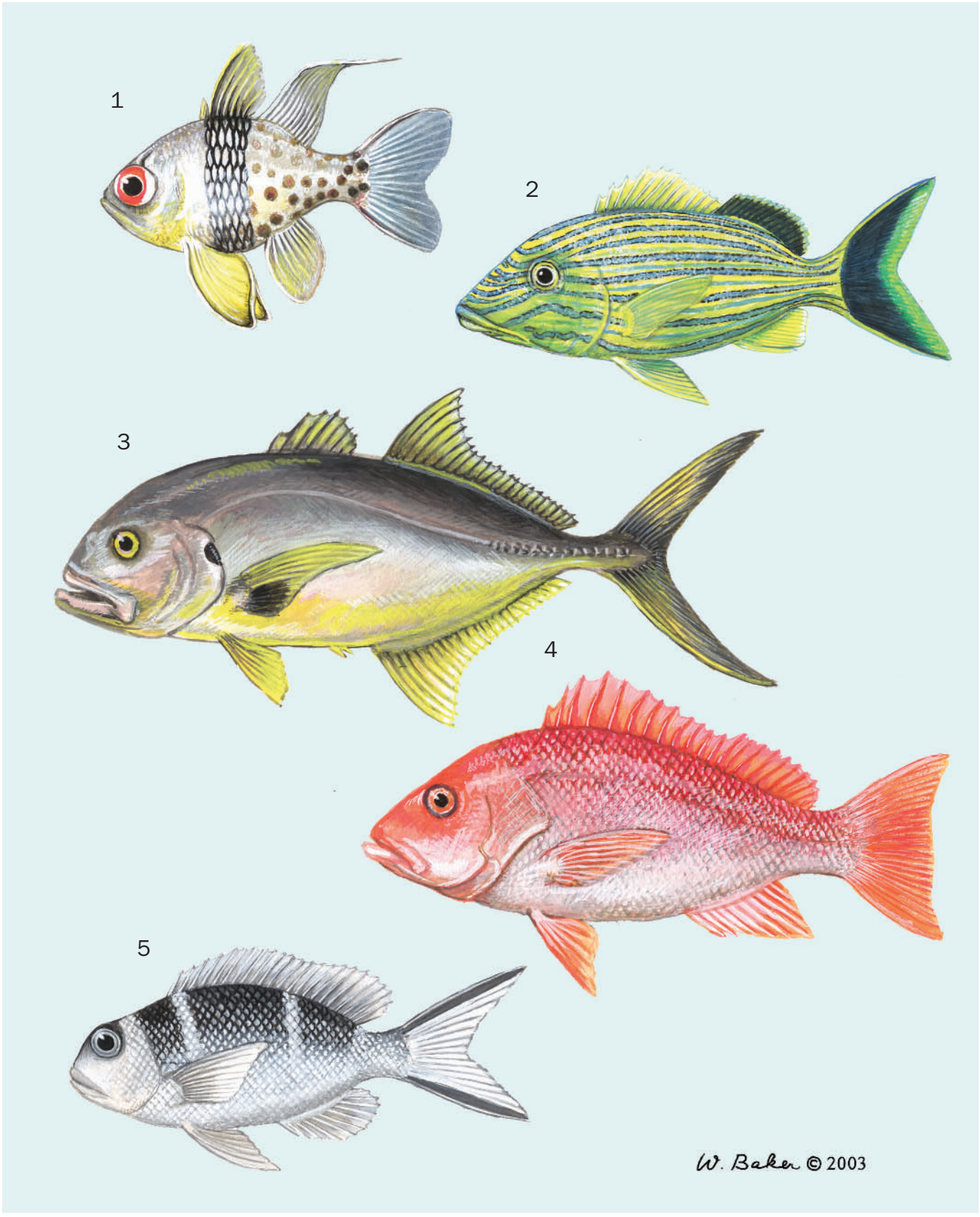
Conservation status

The 2002 IUCN Red List categorizes numerous species from these families as Critically Endangered (5 species), Endangered (3 species), or Vulnerable (12 species). In addition, fishes important to commercial (food and aquarium), subsistence, and recreational fisheries, either as target species or as bycatch, are vulnerable to overfishing.

Significance to humans

Members of the following families are important commercial, recreational, and subsistence fisheries species: Ambassidae, Polyprionidae, Serranidae, Callanthiidae, Glaucosomatidae, Priacanthidae, Apogonidae, Sillaginidae, Malacanthidae, Rachycentridae, Carangidae, Menidae, Leiognathidae, Bramidae,

Lutjanidae, Caesionidae (also used as bait in tuna fisheries), Lobotidae, Gerreidae, Haemulidae, Dinopercidae, Sparidae, Lethrinidae, Nemipteridae, Polynemidae, and Sciaenidae. Species important in the aquarium trade include members of the following families: Ambassidae, Serranidae, Grammatidae, Callanthiidae, Pseudochromidae, Plesiopidae, Opistognathidae, Apogonidae, Malacanthidae, Lutjanidae, Caesionidae, Haemulidae, Sparidae, Lethrinidae, Nemipteridae, and Sciaenidae. Some species within a few families are also cultured for food or for release in the wild to enhance recreational fisheries (e.g., Serrandiae, Sillaginidae, Lutjanidae, and Sparidae). Others, particularly larger individuals of certain species, have been implicated in cases of ciguetara poisoning in humans.



1. Pajama cardinalfish (*Sphaeramia nematoptera*); 2. Bluestriped grunt (*Haemulon sciurus*); 3. Crevalle jack (*Caranx hippos*); 4. Northern red snapper (*Lutjanus campechanus*); 5. Humpnose big-eye bream (*Monotaxis grandoculis*). (Illustration by Wendy Baker)

1. Blacksaddled coral grouper “tiger morph” (*Plectropomus laevis*); 2. Sixline soapfish (*Grammistes sexlineatus*); 3. Goggle eye (*Priacanthus hamrur*); 4. Red drum (*Sciaenops ocellatus*); 5. Nassau grouper (*Epinephelus striatus*). (Illustration by Emily Damstra)

Species accounts

Pajama cardinalfish
Sphaeramia nematoptera

FAMILY
Apogonidae

TAXONOMY
Sphaeramia nematoptera (Bleeker, 1856), Manado, Sulawesi (Celebes), Indonesia.

OTHER COMMON NAMES
English: Coral cardinalfish, polka-dot cardinalfish; Japanese: manjû-ishimochi; Malay: Capungon; Tagalog: Suga.

PHYSICAL CHARACTERISTICS
Body somewhat deep with large eyes; large, extended fins; and a slightly forked caudal fin. The skin has bioluminescent bands. There are two dorsal fins; the first has 7 spines and the second 1 spine and 9 soft rays. The anal fin has 2 spines and 9 soft rays. There are 12–14 soft rays on the pectoral fin. The head and gills are yellow that grades into a broad brown band that extends from the dorsal fin to the posterior portion of the pelvic fin. Posterior to the band, the body is a pale luminescent white with numerous brown spots. The second dorsal fin, anal fin, and caudal fin are clear but edged with luminescent white. The anterior portion of the pelvic fin is yellow and the eye is bright red. This species is sexually dimorphic for body size, with females slightly larger on average but males with deeper bodies and larger heads. Grows to 3.1 in (8 cm) in total length.

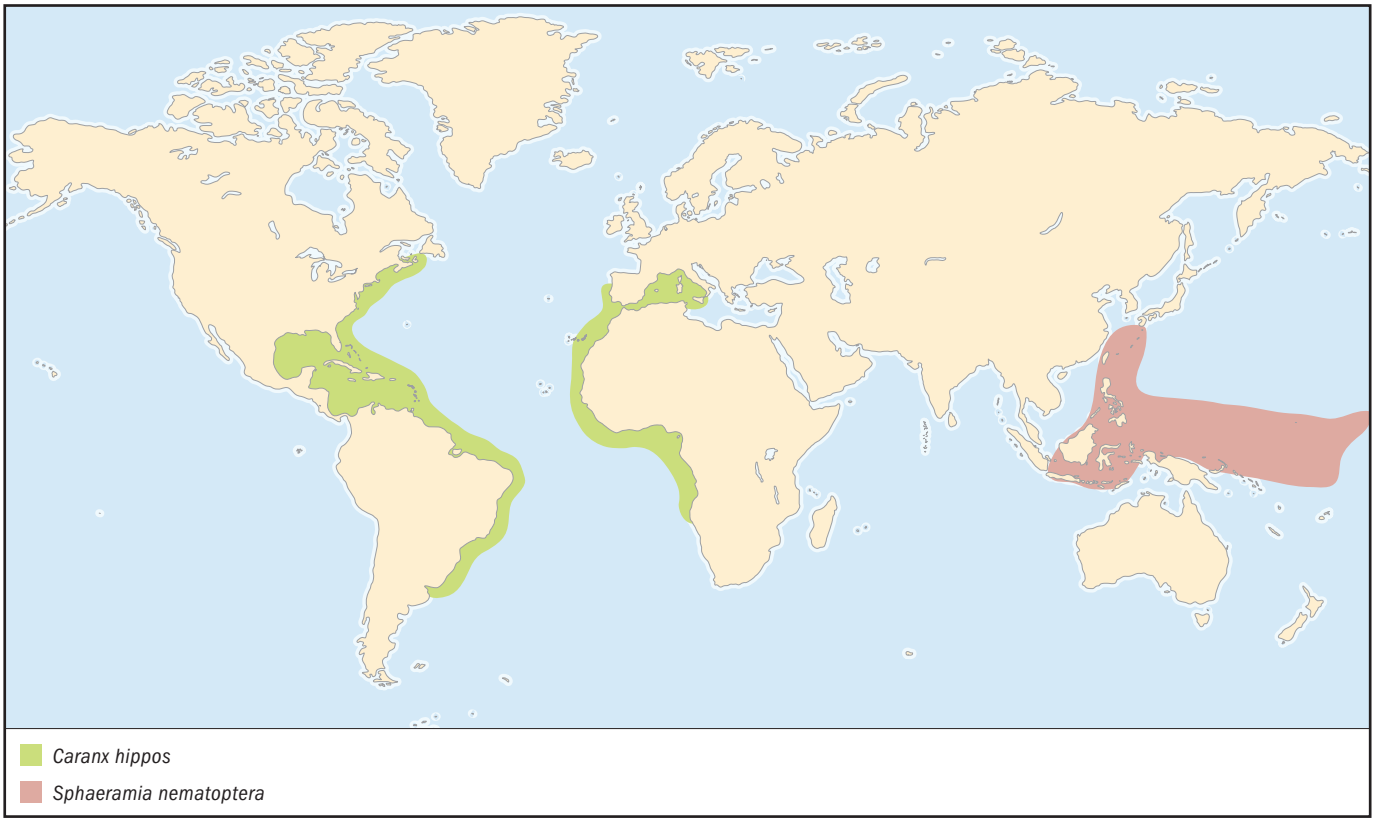
DISTRIBUTION
Western Pacific, from Java, Indonesia, east to New Guinea, Palau, and Pohnpei in the Caroline Islands, and north to the Mariana and Ryukyu islands.

HABITAT
Usually found in protected bays, lagoons, and backreefs among the branches of *Porites* corals.

FEEDING ECOLOGY AND DIET
Feeds upon plankton in the water column. Preyed upon by larger roving and ambush predatory fishes.

BEHAVIOR
Aggregates in coral branches during daylight and disperses along the bottom at night.

REPRODUCTIVE BIOLOGY
Not well known in nature. May possess a promiscuous mating system with multiple spawning events during a season. Males incubate the eggs orally. The incubation period varies with water temperature; eggs of a congener hatched after eight days at water temperatures of 80–86° F (27–30° C). The larvae are pelagic. This species has also been bred in captivity.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular in the aquarium trade. ◆

Crevalle jack
Caranx hippos

FAMILY
Carangidae

TAXONOMY
Caranx hippos (Linnaeus, 1766), Carolina, United States.

OTHER COMMON NAMES
English: Jack crevalle, common jack, couvalli jack; French: Carangue crevalle; Spanish: Cavalla; Portuguese: Coa.

PHYSICAL CHARACTERISTICS
Body deeply compressed with a steep forehead, two dorsal fins, a narrow caudal peduncle, and a slender forked caudal fin. The caudal peduncle is reinforced with a series of scutes (25–42) formed from modified bone. There are 9 spines in the first dorsal fin and 19–21 soft rays in the second dorsal fin, and 3 spines and 15–17 soft rays in the anal fin. The second dorsal fin and the anal fin are both elevated. The eye has an adipose eyelid. Scales are cycloid and small. Body color is silvery to brassy, the dorsal surface olive or bluish green, and the caudal fin yellowish. There is a black spot on the gill cover at equal height with the eye. Grows to about 49 in (124 cm) in total length.

DISTRIBUTION
In the eastern Atlantic, from Portugal to Angola and into the western Mediterranean. In the western Atlantic, from Nova Scotia south to Uruguay and including the Gulf of Mexico; absent from the eastern Lesser Antilles.

HABITAT
In the lower water column on coral and rocky reefs, over mud, sand, and rubble bottoms, and into brackish estuaries, canals, and rivers.

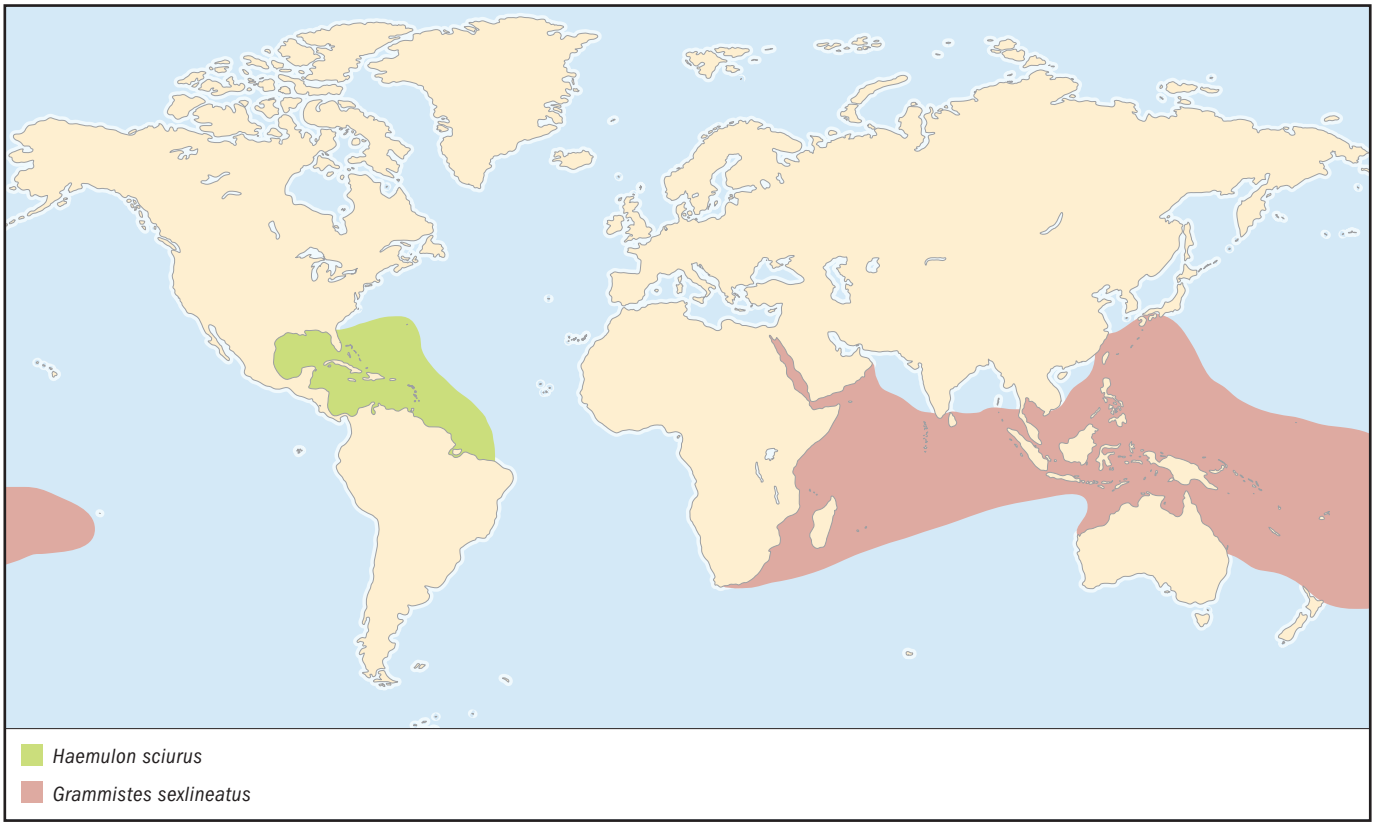
FEEDING ECOLOGY AND DIET
Highly predatory, feeding upon smaller fishes, shrimp, crabs, and other macroinvertebrates. Juveniles may be preyed upon by larger fishes, wading birds, and sea birds, while adults may be taken by sharks or other large predatory fishes.

BEHAVIOR
Forms aggregations, although larger individuals are often solitary or paired.

REPRODUCTIVE BIOLOGY
Forms spawning aggregations at predictable locations during peak times annually, usually April thru May. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Highly prized as a game fish but also harvested by commercial and subsistence fisheries; also collected for display in larger aquaria. May be ciguatoxic in some areas. ◆



Bluestriped grunt
Haemulon sciurus

FAMILY
Haemulidae

TAXONOMY
Haemulon sciurus (Shaw, 1803), Antilles, Caribbean.

OTHER COMMON NAMES
English: Golden grunt, yellow grunt; French: Gorette catire; Spanish: Ronco catire; Dutch: Neertje; Portugese: Biquara.

PHYSICAL CHARACTERISTICS
Typically perch or bass-like; the body color is yellow with a series of blue stripes that run from the head to the caudal peduncle. Fins are yellowish, except for the posterior portion of the dorsal fin and also the caudal fin, which are black. The caudal fin margin may be yellow. There are 12 spines and 16–17 soft rays in the dorsal fin, and 3 spines and 9 soft rays in the anal fin. The caudal fin is emarginate. Grows to about 18 in (46 cm) in total length.

DISTRIBUTION
Western Atlantic, from Florida south to northern Brazil, west through the Gulf of Mexico and throughout the Caribbean.

HABITAT
Juveniles are found in *Thalassia* sea grass beds. Adults occur over coral and rocky reefs and near drop-offs. Depth range is 3–98 ft (1–30 m).

FEEDING ECOLOGY AND DIET
Mainly nocturnal predators of crustaceans, bivalves, and small fishes.

BEHAVIOR
Forms small groups that migrate twice daily along predictable routes at dawn and dusk. Knowledge of the locations of these routes has been demonstrated to be transmitted culturally by older fishes to younger ones in a related species.

REPRODUCTIVE BIOLOGY
Little is known. Likely forms spawning aggregations at predictable locations annually (autumn through spring, probably around the full moon); spawning is doubtless pelagic, as are the eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A minor commercial and recreational species; also collected for the aquarium trade and for public aquaria. Ciguatoxic in some areas. ◆

Humpnose big-eye bream
Monotaxis grandoculis

FAMILY
Lethrinidae

TAXONOMY
Monotaxis grandoculis (Forsskål, 1775), Jidda, Saudi Arabia, Red Sea.

OTHER COMMON NAMES
English: Big-eye barenose, big-eye bream; French: Emperor bossu; Japanese: Yokushima-kurodai.

PHYSICAL CHARACTERISTICS
The body is oblong with a strongly convex profile of the head anterior to the eye; the snout is steeply sloped. The mouth is relatively large with pronounced canines and molars that are used for grasping and crushing prey, respectively. The eye is large; juveniles have a prominent black stripe through the eye. The dorsal fin has 10 slender spines and 10 soft rays, the anal fin has 3 spines and 9 soft rays, and the pectoral fin has 14 rays. The caudal fin is forked in adults and somewhat lunate in juveniles. Body color is light brown to bluish grey; ventral surfaces are white. Three prominent black or dark brown saddles cover the flank dorsally. Fins and the caudal peduncle range from yellow or reddish orange to clear or dusky. The lobes of the caudal fin may be pink in adults. Able to switch between dark and light color forms by behavioral control, usually in response to the color of the sea bottom. Grows to 23.6 in (60 cm) in total length.

DISTRIBUTION
Indo-West Pacific, from the Red Sea and East Africa east to the Hawaiian Islands, southeast to French Polynesia, south to northern Australia, and north to southern Japan.

HABITAT
Tropical coral and rocky reefs, over coral, sand, and rubble.

FEEDING ECOLOGY AND DIET
Feeds at night upon gastropods, echinoderms (mainly sea stars and brittle stars, but also sea cucumbers), crabs, polychaete worms, and tunicates.

BEHAVIOR
Often solitary in the water-column; juveniles closer to the bottom. Adults also form large aggregations that swim lazily over the reef or reef slope.

REPRODUCTIVE BIOLOGY
Little is known. Probably forms spawning aggregations and produces pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN.

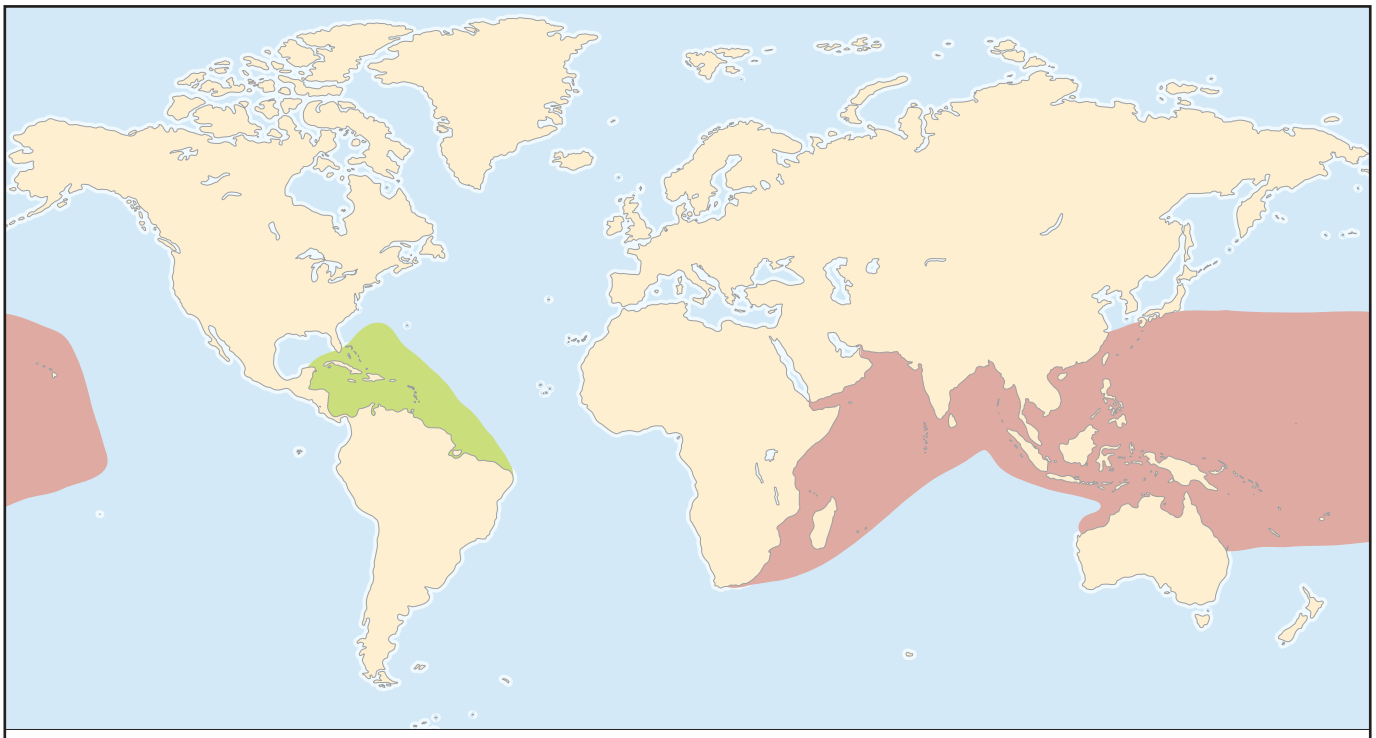
SIGNIFICANCE TO HUMANS
Taken in commercial, subsistence, and recreational fisheries; juveniles are collected infrequently for the aquarium trade, and adults are collected for large public aquaria. May be ciguatoxic in some areas, such as the Marshall Islands. ◆

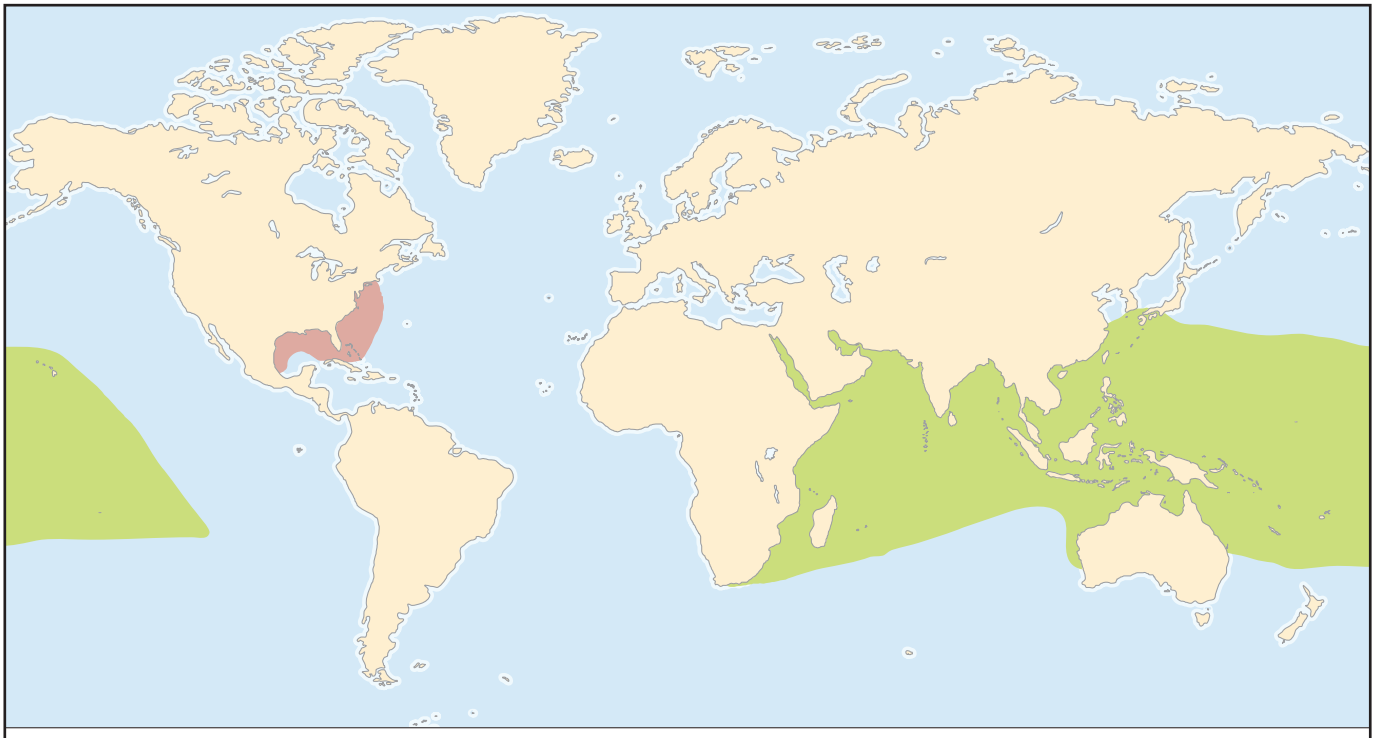
Northern red snapper
Lutjanus campechanus

FAMILY
Lutjanidae

TAXONOMY
Lutjanus campechanus (Poey, 1860), Campeche, Mexico.

OTHER COMMON NAMES
English: Red snapper; French: Vivaneau campèche; Spanish: Pargo de golfo.


Epinephelus striatus
Monotaxis grandoculis


Priacanthus hamrur
Lutjanus campechanus

PHYSICAL CHARACTERISTICS
Typically bass-like in appearance, with a deep body, a single dorsal and anal fin, and an emarginate caudal fin. There are 10 spines and 14 soft rays in the dorsal fin, 3 spines and 8–9 soft rays in the anal fin, and the pectoral fin is elongate, almost reaching the anus, with 17 rays. The eyes are relatively small. Body color is red with orangish red fins. Grows to about 39 in (100 cm) in total length.

DISTRIBUTION
Western Atlantic, from Massachusetts (rarely) south through the Carolinas to Florida, west through the Gulf of Mexico to the Yucatan Peninsula and southeast to the northern edge of Cuba.

HABITAT
Juveniles frequent inshore waters, usually over sand or mud bottoms. Adults prefer rocky bottoms. Depth range of adults is 33–623 ft (10–190 m).

FEEDING ECOLOGY AND DIET
Accomplished predator that feeds upon smaller fishes, crabs, shrimps, cephalopods, polychaete worms, and gastropods and urochordates in the water column.

BEHAVIOR
Swims alone or in aggregations just above the bottom. May be idle during daylight and active at night.

REPRODUCTIVE BIOLOGY
Dioecious; there is no sex change. Males and females migrate to specific locations to form spawning aggregations between the months of April and December. Spawning is pelagic, as are the eggs and larvae. Eggs hatch in about a day.

CONSERVATION STATUS
Not listed by the IUCN but has been shown to be vulnerable to overfishing as a primary target species and, for juveniles, as bycatch in shrimp trawls. Fisheries are regulated in U. S. waters.

SIGNIFICANCE TO HUMANS
Important commercial and recreational species. ◆

Goggle eye
Priacanthus hamrur

FAMILY
Priacanthidae

TAXONOMY
Priacanthus hamrur (Forsskål, 1775), Jidda, Saudi Arabia, Red Sea.

OTHER COMMON NAMES
English: Lunar tail bigeye, moontail bullseye; French: Beauclaire miroir; Japanese: Hoseki-kintoki.

PHYSICAL CHARACTERISTICS
Body deep and compressed, with rough scales, large eyes, relatively large fins, and a caudal fin that is slightly emarginate. There are 10 spines and 14–15 soft rays in the dorsal fin, and 3 spines and 14–15 soft rays in the anal fin. Body color is a red or coppery red that fades to a mottled pattern of silver and red in darkness. Grows to 18 in (45 cm) in total length.

DISTRIBUTION
Indo-West Pacific, from the Red Sea and East Africa east to the Marquesas and Mangareva in French Polynesia, and Easter Island. Also found from southern Japan in the Northern Hemisphere to Australia and Lord Howe Island in the Southern Hemisphere.

HABITAT
Frequents ledges, crevices, caves, and the lower water column of outer reef slopes, passes, and deep lagoons; also found around pinnacles in lagoons and offshore patch reefs.

FEEDING ECOLOGY AND DIET
Feeds mainly at night upon smaller fishes, crustaceans, cephalopods, and larger zooplankton. Preyed upon by larger predatory fishes.

BEHAVIOR
Often solitary, hovering in or next to shelter or in the lower water column in daylight but more active at night. Changes color from red to silver or mottled-silver and red in darkness. The large eyes of this species are advantageous in low-light conditions, both for feeding and predator avoidance.

REPRODUCTIVE BIOLOGY
Little is known. May form spawning aggregations. The eggs and larvae are reportedly pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken in commercial and subsistence fisheries and incidentally in recreational fisheries. Sometimes collected for larger aquaria. ◆

Nassau grouper
Epinephelus striatus

FAMILY
Serranidae

TAXONOMY
Epinephelus striatus (Bloch, 1792), Martinique, West Indies.

OTHER COMMON NAMES
French: Mérou rayé; Spanish: Cherna criolla.

PHYSICAL CHARACTERISTICS
Robust body with sloping forehead, large fins, and a somewhat truncated caudal fin (rounded in juveniles). There are 11–12 spines, the third or fourth being the longest, and 16–18 soft rays in the notched dorsal fin, and 3 spines and 8 soft rays in the anal fin. Body color is tawny brown (shallow water) to pinkish brown or red (deeper water). There are alternating dark (brown or olive) and pale bands along the flanks and onto the dorsal fins, with similar dark bands extending along the head to the snout, a dark saddle on the upper caudal peduncle, and dark spots around the eye. Two color phases, pale and dark, are controlled behaviorally, and change between one and the other is rapid. Grows to about 47 in (120 cm) in total length.

DISTRIBUTION
Western Atlantic, from Bermuda and Florida south to the Bahamas and the Yucatan Peninsula, throughout the Caribbean,

and south to northern Brazil. Absent from most of the Gulf of Mexico.

HABITAT
Juveniles usually found in sea grass beds, while adults prefer coral and rocky reefs to a depth of 295 ft (90 m).

FEEDING ECOLOGY AND DIET
An ambush or hunting predator that feeds upon smaller fishes, crustaceans (mainly crabs), and large mollusks. Vulnerable to natural predation mainly as juveniles; adults vulnerable to larger predators such as sharks and large barracudas.

BEHAVIOR
Generally solitary as adults, although may form aggregations (especially for spawning). Site specific but probably with a large territory. Changes color pattern from one phase to the other depending upon circumstances. Not especially wary and may be friendly towards divers.

REPRODUCTIVE BIOLOGY
Matures at about 16–18 in (40–45 cm) in standard length, somewhere between 4–8 years of age. A protogynous hermaphrodite, but primary males have also been found. Spawns pelagically in large aggregations that form at specific locations annually depending upon lunar phase and water temperature. Courtship occurs within the aggregation just prior to or after sunset with spawning soon after sunset. The two color phases are used at this time to indicate submissive roles that reduce aggregation and promote courtship behavior. Females assume a dark color phase during courtship and lead spawning events. Events occur usually in subgroups of 3–25 fish, with a spawning ascent well into the water column. Eggs and larvae are pelagic.

CONSERVATION STATUS
Listed as Endangered on the IUCN Red List. Spawning aggregations of this species should be protected and fisheries harvests greatly restricted.

SIGNIFICANCE TO HUMANS
Important in commercial, subsistence, and recreational fisheries but now severely overfished throughout most of its range. Especially vulnerable when in spawning aggregations. Also collected for large aquaria. May be ciguatoxic in some areas. ◆

Sixline soapfish
Grammistes sexlineatus

FAMILY
Serranidae

TAXONOMY
Grammistes sexlineatus (Thunberg, 1792), type locality not specified.

OTHER COMMON NAMES
English: Black and white–striped soapfish, gold-striped soapfish, six-stripe soapfish; French: Poisson savon bagnard.

PHYSICAL CHARACTERISTICS
Body typically grouper or perch-like but somewhat stout. The head is relatively large. There are 7 spines and 13–14 soft rays in the dorsal fin and 2 spines and 9 soft rays in the anal fin. The caudal fin is truncate. The base color is dark brown to black with a series of yellow stripes running from the snout back to the caudal peduncle. With age, some stripes may break up into dashes. Juveniles have small spots. Fins are pinkish in color. Grows to about 12 in (30 cm) in total length.

DISTRIBUTION
Indo-West Pacific, from the Red Sea east to the Marquesas and Mangareva Islands, north to southern Japan and south to northern New Zealand.

HABITAT
This species occurs on coral and rocky reefs, usually in or near caves and under ledges to a depth of 425 ft (130 m).

FEEDING ECOLOGY AND DIET
Generally an ambush predator, and quite voracious as it feeds upon smaller fishes and crustaceans. May be preyed upon by larger predatory fishes but usually rejected immediately because of the secretion of grammistin, a toxin secreted from glands in the skin that is used as an antipredator mechanism.

BEHAVIOR
Usually solitary, preferring to hide during daylight while foraging at night.

REPRODUCTIVE BIOLOGY
Little is known. Likely a protogynous hermaphrodite with a haremic mating system, pair spawning, and pelagic eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An interesting aquarium species, although because of its voracious appetite it must be kept with much larger fishes. Also taken as a minor commercial and subsistence species in some localities. May be ciguatoxic in some areas. ◆

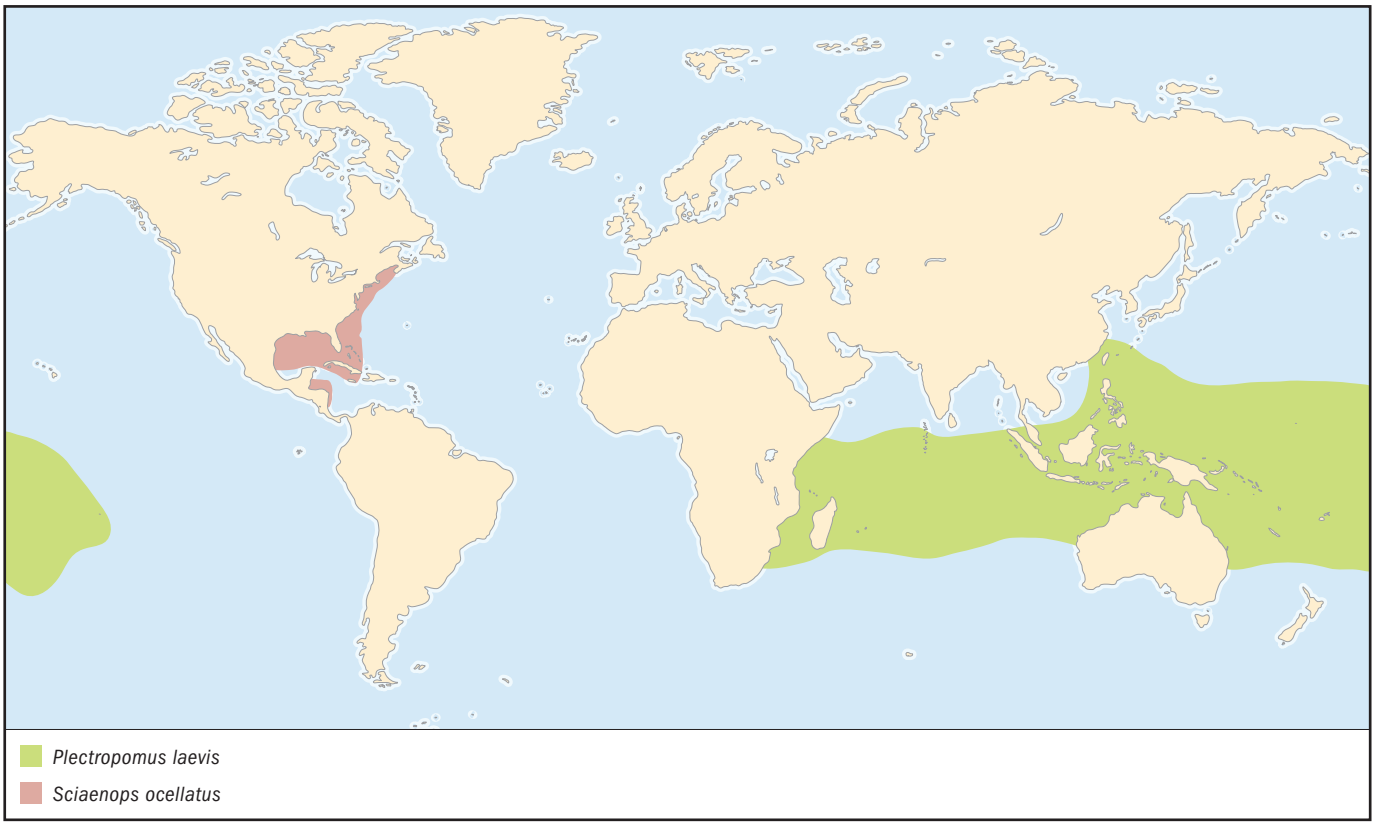
Blacksaddled coral grouper
Plectropomus laevis

FAMILY
Serranidae

TAXONOMY
Plectropomus laevis (Lacepede, 1801), type locality not specified.

OTHER COMMON NAMES
English: Blacksaddled coral trout, giant coral trout, tiger coral trout; French: Mérou sellé.

PHYSICAL CHARACTERISTICS
Body elongate and robust, with the outer margin of the anal fin straight, and a large and slightly emarginate caudal fin. The mouth is relatively large with prominent canines. There are 8 spines and 11 soft rays in the dorsal fin, 3 spines and 8 soft rays in the anal fin, and 16–18 rays in the pectoral fin. This species has two color phases. The "tiger" or pale phase consists of a base color of white with four black bars or saddles, some incomplete, along the flank, yellow fins and mouth parts, and small blue spots with dark edges on the caudal penduncle and caudal fin. The dark phase is reddish brown with many small blue spots with dark edges scattered over the body and fins, and less prominent bars along the flanks. Grows to 39 in (100 cm) in total length.



DISTRIBUTION
Indo-West Pacific, from Kenya and Mozambique east to the Tuamotu Archipelago in Polynesia, north to the Ryukyu Islands of Japan, and south to Queensland in Australia; absent from the Red Sea and Persian Gulf.

HABITAT
Juveniles are often found in turbid areas of deeper lagoons and back reefs, while adults prefer the clear water of seaward reefs, lagoons, and passes. Will utilize holes and crevices in the reef for shelter.

FEEDING ECOLOGY AND DIET
An efficient predator that feeds primarily upon smaller fishes and, to a lesser extent, large crustaceans. Larger individuals take larger prey, however, and often these are fishes (e.g., parrotfishes, large wrasses, surgeonfishes) that may be up to nearly half their body length in size.

BEHAVIOR
Juveniles and young adults may be somewhat gregarious and often hover above the bottom, but will retreat to shelter when threatened. Larger adults utilize habitat as shelter but may be found patrolling territories or home ranges.

REPRODUCTIVE BIOLOGY
Protogynous hermaphrodite that forms spawning aggregations prior to courtship and spawning. Spawning occurs between October and November on the northern Great Barrier Reef. Spawning is pelagic, as are the eggs and larvae.

CONSERVATION STATUS
Not listed by the IUCN but potentially vulnerable to overfishing at some localities.

SIGNIFICANCE TO HUMANS
A species of particular importance to commercial, recreational, and subsistence fisheries. Large individuals may be highly ciguatoxic. ◆

Red drum
Sciaenops ocellatus

FAMILY
Sciaenidae

TAXONOMY
Sciaenops ocellatus (Linnaeus, 1766), Carolina, (United States).

OTHER COMMON NAMES
English: Redfish, channel bass; French: Tambour rouge; Spanish: Corvinón ocelado.

PHYSICAL CHARACTERISTICS
Body elongate with a somewhat large head, subterminal mouth, two dorsal fins, and a truncate caudal fin. The anal fin has two spines and the lateral line is continuous. Body color is coppery-orange to light red; ventral surfaces are white. The upper caudal peduncle has a prominent black spot. Grows to about 61 in (155 cm) in total length, although less so inshore compared to fishes living around barrier islands.

DISTRIBUTION
Western Atlantic, from Massachusetts south to southern Florida and west to northern Mexico in the Gulf of Mexico.

HABITAT
Inshore coastal waters and estuaries, over sand, mud, or oyster-shell bottoms, among flooded marsh grasses, or in the surf zone.

FEEDING ECOLOGY AND DIET
Forages along the bottom in search of crustaceans, mollusks, and smaller fishes; will also form aggregations and attack schools of baitfish in shallow water.

BEHAVIOR
Occurs singly or in aggregations. Communicates by using muscle contractions to make a drumming noise that is amplified by the swim bladder.

REPRODUCTIVE BIOLOGY
Forms spawning aggregations, mainly from August through November. Males produce a drumming noise when courting females. Eggs are scattered and the larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN. Fisheries are heavily regulated in most places, as this species was severely overfished in the Gulf of Mexico during the 1980s.

SIGNIFICANCE TO HUMANS
Once important in commercial fisheries but less so by the beginning of the twenty-first century. An important recreational species that is collected also for large public aquaria. Raised in aquaculture.

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Society for the Conservation of Reef Fish Aggregations. c/o Department of Ecology and Biodiversity, University of Hong Kong, Pok Fu Lam Road, Hong Kong, China. E-mail: scrfa@hkucc.hku.hk Web site: <http://www.scrfa.org/>

Other

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Terry J. Donaldson, PhD

Labroidei I

(Cichlids and surfperches)

Class Actinopterygii
Order Perciformes
Suborder Labroidei
Number of families 2

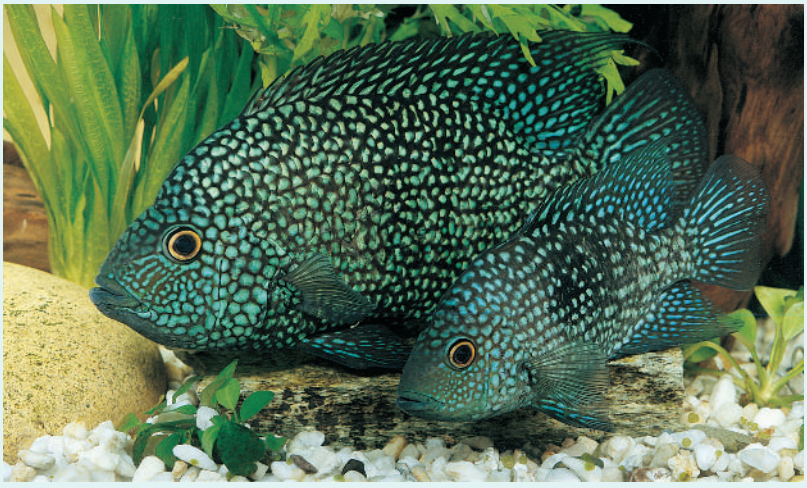


Photo: Tampico cichlid (*Herichthys carpintis*) adult and juvenile. (Photo by Hans Reinhard/Okapia/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The families Cichlidae (cichlids) and Embiotocidae (surfperches) have traditionally been grouped in the suborder Labroidei, along with Labridae (wrasses), Scaridae (parrotfishes), Pomacentridae (damselfishes), and Odacidae (western Pacific butterfishes). These groups were first suggested to share a common ancestry by Müller in 1843. All possess a pharyngeal jaw apparatus (a second set of jaws in the throat) that aids in the processing of food, and the morphological characters supporting their close relationship are all a part of this functional complex. Characters used to unite labroids include fused fifth ceratobranchials that bear teeth, a muscle sling suspending the lower pharyngeal jaw from the skull, an articulation between the upper pharyngeal jaws and the base of the skull without intervening muscle, and an undivided sheet of sphincter esophagi muscle. The reliability of these characters has been questioned, and the reality of the Labroidei has been challenged for several reasons. One is that none of the characters are unique to labroids (in fact, a whole suite of pharyngeal jaw features are found in the quite distantly related Beloniformes); another is that not all labroids present all the characters. In addition, characters supporting the Labroidei that are independent of the pharyngeal jaw apparatus, and perhaps less strongly influenced by selective forces related to food processing, have eluded detection. Given these challenges, it isn't surprising that recent molecular studies have failed to uphold the Labroidei as a natural group.

Nonetheless, this chapter considers two of the traditional labroid families, the cichlids and surfperches. Surfperches are temperate, almost entirely marine fishes found only in the northern Pacific, and are represented by 13 genera and 24 species. Cichlids are mostly tropical freshwater fishes, with a distribution on fragments of the supercontinent of Gondwana. There are about 105 genera of cichlids and 1,405 described species, although some estimates place the total number of cichlid species to be in excess of 2,500 if a full accounting is made of the exceptional species diversity in the three African Great Lakes. Different geologic processes and time scales have shaped these three lakes and their species flocks. Two of the lakes, Malawi and Tanganyika, formed in a rift created by plate movements that are slowly ripping apart the African continent. Lake Malawi is roughly 700,000 years old and contains 500–1,000 cichlid species; Lake Tanganyika is 9–12 million years old and contains about 200 cichlid species. Lake Victoria, formed by processes of mountain building that blocked the flow of rivers draining eastern Kenya, was probably entirely dry as recently as 12,400 years ago, leaving precious little time for the subsequent evolution of its 500 or so haplochromine cichlid species from a single ancestral species.

Evolutionary biologists have been intrigued by the question of how so many cichlid species evolved together in African lakes. Clearly, the ability of cichlids to finely partition resources provides some explanation, but the lakes themselves also play a role. Lake Victoria is relatively shallow and turbid, with few rocky microhabitats along its shoreline, but the two rift lakes are clear and deep, with abundant patches of rocky microhabitat scattered along their shores. Within Tanganyika, there are three distinct communities: the pelagic, containing six fish species; the benthic, with 80 fish species; and most diverse, the littoral, with 207 species of fishes. Most of the species diversity is restricted to inshore regions. Malawi's piscine endowment is similarly biased; so species poor are the pelagic waters in comparison with the littoral rocky communities that two zooplanktivorous species of the genus *Diplotaxodon* make up 71% of the open-water fish biomass. In Malawi and Tanganyika, populations in rocky littoral habitats separated by sandy bottom and deepwater barriers wider than 1.2 mi (2 km) exhibit little or no gene flow. Thus, a model of microallopatric speciation may be appropriate for the rift lakes, whereby the numerous and fragmented littoral rocky habitats, coupled with attributes of some of the cichlids, such as

Kribensis pair (*Pelvicachromis pulcher*) with young. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

resource specialization and adherence to circumscribed territories, have fostered explosive speciation. Another speciation mechanism, sexual selection, has been considered most important in Victoria due to its paucity of isolated microhabitats, and may also be important in the rift lakes.

Age differences between the lakes are also manifest in the cichlid species flocks. The two younger lakes, Malawi and Victoria, contain relatively more homogenous assemblages of strictly mouth-brooding cichlids. In contrast, Lake Tanganyika contains a very diverse assemblage of both mouth brooders and substrate spawners descended from numerous colonization events. In a 1998 paper, Sturmbauer contrasted the relatively young lake Victoria species flock, which lacks extreme morphotypes and has many intermediate species, with the ancient Lake Tanganyika flock, characterized by few intermediates and high morphological distances between species, and proposed that the two lakes represent opposite ends of a species flock evolutionary continuum. He suggested that in older lakes with mature flocks (as in Tanganyika), very diverse communities sharing most of their species will predominate, because dispersal events (facilitated by lake level fluctuations) have, over long stretches of time, mixed together species that arose in isolation. Consequently, lesser competitors in shared niches will have alternately diverged or perished.

Despite the present diversity of cichlids, both cichlids and surfperches are poorly represented in the fossil record. Fossil surfperches are first known from the upper Miocene epoch (5–10 million years ago), from the Monterey Formation in California. Only a few species of fossil cichlids are known, the earliest of which are 45 million years old (Eocene epoch) from Tanzania, East Africa. Cichlid material from Maranhao, Brazil, may also date from the Eocene, and putatively cichlid material of similar age has been found in Vicenza, Italy. If, as many researchers suggest, the present geographic distribution of cichlids is an artifact of their being widely distributed on the supercontinent of Gondwana, then cichlids must be at least 130 million years old, leaving an inexplicable gap of 85 million years in the fossil record. This has led some to argue that cichlids are actually a younger group that has dispersed across marine barriers to achieve their present distribution, an argument supported by the ability of several cichlid species to survive in sea water and the fact that cichlid distribution is not strictly Gondwanan.

Physical characteristics

Surfperches are relatively deep bodied, laterally compressed fishes with an undivided series of lateral line scales. They achieve lengths of 17.5 in (45 cm). All surfperches have cycloid scales, a deeply forked caudal fin, and three anal fin spines. Most species have scales extending onto the dorsal fin. Although many species are uniformly silvery, others have blue, black, or reddish stripes and bars. Cichlids are more variable, presenting both cycloid and ctenoid scales, a divided lateral line scale series (except in the African riverine genera *Teleogramma* and *Gobiocichla*), numerous fin shapes and lengths (the smallest species is 1 in [2.5 cm], while the largest is 36 in [91.4 cm]), and anywhere from three to 15 anal fin spines. Cichlids are also unusual in that they have only a single nostril on each side of the head, unlike most teleosts, which have two pairs of nostrils.

Cichlids exhibit an impressive range of morphological diversity: there are dinner plate–shaped discus and cigar-shaped pike-cichlids, horse-faced *Tropheus* that scrape algae from rocks, and canine-endowed *Cichla* that voraciously prey on other fishes. A diversity of tooth morphologies in both the oral and pharyngeal jaws allow cichlids to utilize every conceivable source of food. Cichlids can be drab colored or come in brilliant hues, and many exhibit magnificent color patterns that are rivaled only in coral-reef fishes. Despite their variability, however, cichlids share numerous distinctive morphological characters supporting the family as a natural group derived from a common ancestor. For instance, all cichlids have a transversus dorsalis muscle partitioned into four parts, a functionally decoupled premaxilla and maxilla, microbranchiospines on the outer faces of the gill arches, and an expanded head of the fourth epibranchial.

Distribution

Surfperches are distributed in coastal areas of the North Pacific: three species are found around Japan and Korea, and 21 species are found in North America from Alaska to the Baja Peninsula. One species, the shiner perch (*Cymatogaster aggregata*), enters brackish and fresh waters. Another species, the tule perch (*Hysterocarpus traskii*) is entirely confined to freshwater lakes and rivers in California.

Cichlids are distributed in the tropical and subtropical regions of most Gondwanan fragments, including much of South America and Africa, Madagascar, India, and Sri Lanka. They also occur naturally in Syria, Iran, Israel, Central America, North America (Texas), and the West Indies. Human introductions have led to the establishment of numerous cichlid

species in localities outside their natural range. Owing to their popularity in aquaculture, the tilapiines in particular have been spread around the globe, often with devastating consequences for endemic fishes. Various tilapiines now thrive in the fresh waters of Madagascar, Mexico, Florida, and much of Southeast Asia, as well as the coastal waters of southern California.

Habitat

Surfperches are mostly restricted to inshore marine environments. Many species are found in the surf near sandy beaches, but members of the family also frequent sea-grass beds, rocky outcroppings, and piers. Less frequently, surfperches are known to enter brackish and fresh waters, and one species lives its whole life in lakes and rivers.

Cichlids also exhibit a wide salinity tolerance, and some species are found in brackish and marine waters. Some cichlids are capable of withstanding rather extreme conditions. For example, some *Oreochromis* species live in high-temperature, high-alkalinity salt lakes in Kenya and Tanzania. Most cichlids are freshwater fishes, however, and members of the family can be found in most every conceivable freshwater habitat within their range, including open waters of lakes, oxygen-deprived depths, rocky inshore areas, aquatic plant beds, swamps, small streams, and large rivers, including rapids habitats.

Behavior

Surfperches are unusual among marine teleosts in that they do not go through a planktonic dispersal stage as eggs or larvae; they are somewhat large when they are born and stay in the general vicinity as they mature. Many cichlids, especially those that occupy specialized lacustrine habitats, behave similarly. Although most cichlids do not defend feeding territories, some cichlids in the African Great Lakes do defend separate feeding and breeding territories. Those that defend feeding territories are predominantly algae feeders, and some herbivorous species subvert such territoriality by forming large schools that barrage an algal mat with a few individuals at a time, diluting the aggression of the territory holder so that algae can be stolen. In captivity, the territoriality and aggression of many cichlids has given the family a particular notoriety among aquarists.

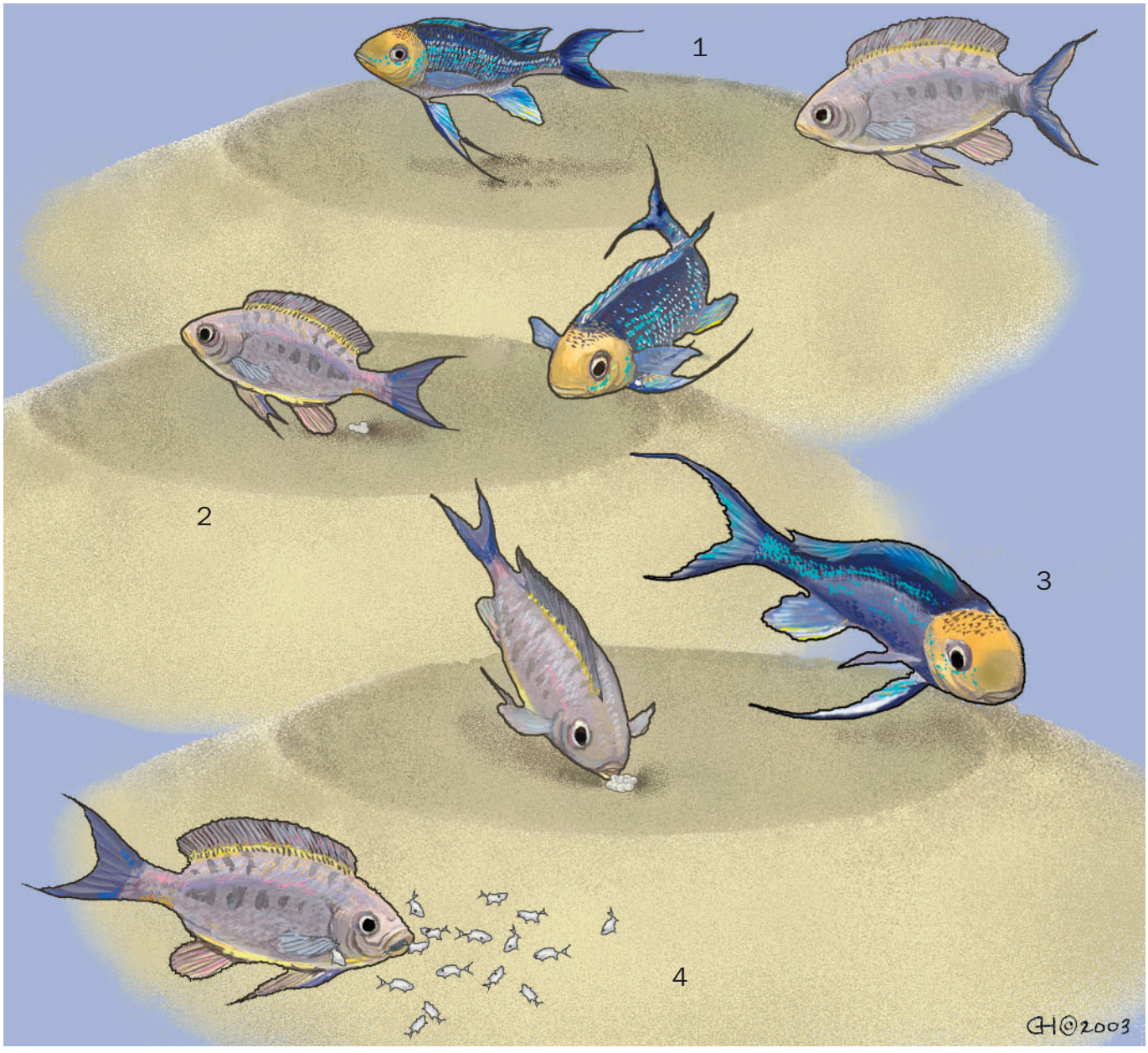
In some cichlids, older siblings assist their parents in guarding new clutches of fry, an investment that can be explained evolutionarily because it increases the share of both the parents' and helpers' genes in the next generation. Consider, however, the few examples of cichlids that help guard the offspring of another species of cichlids, a behavior that at first defies explanation. One tantalizing explanation for such behavior on the part of the moga (*Cichlasoma nicaraguense*), males of which sometimes help guard the fry of the guapote (*C. dovii*), is that larger numbers of piscivorous *C. dovii* help to increase the reproductive success of *C. nicaraguense* by preying upon and reducing the numbers of poor man's tropheus (*Neetroplus nematopus*), a nest-site competitor of the helper species. This interpretation, while intriguing, is still controversial.

Blue discus (*Symphysodon aequifasciata haraldi*) are popular aquarium fish. (Photo by Hans Reinhard/Okapia/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Surfperches feed variously on shrimps, amphipods, crabs, and other crustaceans, as well as mollusks and worms. To feed on such organisms, many surfperches take indiscriminate bites out of the algae and debris found on the bottom, and then winnow out their invertebrate prey within the oropharyngeal cavity, spitting out the remainder. The small kelp perch (*Brachyistius frenatus*) feeds largely on ectoparasites picked off other fishes, and several other surfperches supplement their regular diets by engaging in such cleaning activities.

Cichlid feeding ecologies are extravagantly diverse, and may partly explain the species diversity within the family. Although most cichlids can opportunistically feed on a wide range of foods, they are also specialized to feed on certain types of food with particular efficiency. Of course, many cichlids specialize in hunting other fishes and eating them whole. *Tilapia* is the only genus of African cichlid to specialize on phytoplankton, by collecting the particles (with the assistance of sievelike gill rakers for filtering) in balls of mucous secreted in the mouth and then swallowing them. Deposit feeders take a very similar approach, but with sedimented phytoplankton and even disintegrated hippopotamus droppings. Cichlids who feed on epilithic algae, or aufwuchs, scrape the algae from rocks, typically employing multiple rows of fine teeth used like a file. Periphyton feeders scrape algae off living plants. For example, the giant haplochromis *Hemitilapia*



Breeding habits of the cichlid *Cyathopharynx furcifer*: 1. Male drags long pelvic fins along the bed of the nest, showing female where to lay eggs; 2. Female lays eggs while male waits to fertilize them; 3. Female takes fertilized eggs into her mouth; 4. Hatched fry are released from the female's mouth. (Illustration by Gillian Harris)

oxyrhynchus in Malawi feeds by placing the grasslike leaves of the plant *Vallisneria* between its jaws and nibbling off the algae without damaging the leaf. Singularly robust dentition characterizes leaf choppers, while mollusk feeders have large pharyngeal bones covered with flat, stocky teeth to crush shells. *Labidochromis vellicans* of Malawi, a benthic arthropod feeder, has very long, sharp, outward pointing teeth that resemble forceps, and uses them to pluck insects from the substrate. Alternatively, the greenface sandsifter (*Lethrinops furcifer*) of Malawi has a pointed, protractile mouth and sievelike gill rakers. It rams its head into the sand, filling the buccal cavity, then separates out and swallows insect larvae by expelling the sand across the gill rakers and through its opercular openings. Some species have developed protractile mouths specially suited for inhalant feeding on zooplankton. There exist fin-nipping feeders, and in Victoria and Malawi, species that feed on the eggs and larvae of other mouth brooders. Many species have acquired large molariform teeth on the pharyngeal jaws for crushing the shells of snails. Additionally, in all three African Great Lakes, cichlids with differing tooth morphologies have evolved to feed exclusively on the scales of other fishes; some even mimic the color patterns of their prey to avoid detection.

Interesting selective forces are at work within the scale-feeding Lake Tanganyika genus *Perissodus*. To a greater or lesser degree, all seven species exhibit laterally asymmetrical mouths that are angled either to the right or left, and this trait has a genetic basis. Left-handed individuals nip scales off the right flank of their prey, and vice versa for right-handed individuals. Incredibly, the differential alertness of prey species appears to exert selective pressure on the scale eaters that acts to maintain about equal numbers of left- and right-handed individuals within a population. A study on *Perissodus microlepis* found that whenever one or the other form becomes significantly less abundant, prey species become more vigilant about watching for scale eaters from the side favored by the more abundant form. In this way, the less-abundant form is conferred a selective advantage, and the genetic polymorphism responsible for the two forms is maintained.

Cross-section of a female *Oreochromis* mouth-brooder. (Illustration by Michelle Meneghini)

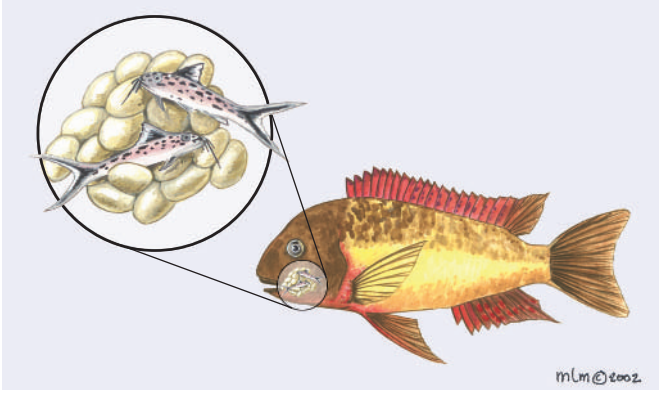
Reproductive biology

Embiotocids are viviparous (give birth to live young), and males have a thickened anterior portion of the anal fin that aids in internal fertilization. They display elaborate courtship behaviors, reminiscent of a small cross-section of the varied courtship behaviors found in cichlids. Some cichlids, for example, members of the genera *Crenicara*, *Sarotherodon*, and *Etroplus*, are capable of changing sex. When a group of females finds themselves without access to a male, the dominant female is able to generate testicular tissue sufficient to fertilize the eggs of the remaining females.

Primitively, cichlids likely formed monogamous pairs, in which both parents guarded eggs laid on the substrate. Cichlids exhibiting this behavior include the Indian etroplines, most Central American taxa, many South American taxa (such as *Pterophyllum* and *Symphysodon*), as well as several African groups (including *Hemichromis* and the lamprologines). Some cichlids have evolved polygamy and mouth brooding as embellishments of the original reproductive mode. Mouth brooders allow the eggs and young to develop inside the safety of the buccal cavity of one or both parents. As the young mature, they make feeding excursions outside, but quickly retreat into the adult's mouth at the first sign of danger. It is fascinating that following egg deposition, females of some mouth-brooding species collect the eggs into their mouths with such alacrity that males do not have time to fertilize them externally. On the anal fin of many such males, however, are conspicuously colored spots, called egg dummies, which bear a remarkable resemblance to the actual eggs. The female notices these spots and nips at them (in an apparent attempt to collect them into her mouth, some have argued), and the male releases sperm at the same time. Thus the eggs are fertilized inside the mouth of the female.

In one instance, a noncichlid has devised a means of capitalizing on the mouth-brooding habit of cichlids at their expense. *Synodontis multipunctatus*, a mochokid catfish, is a brood parasite on several species of mouth-brooding cichlids in Lake Tanganyika. Catfish eggs are concealed among the cichlid eggs during spawning, and are then taken into the mouth of the adult cichlid. As development proceeds, the young catfishes devour the cichlid fry from the safety of the parental buccal cavity, so that ultimately the cichlid parents find themselves caring for a small brood of catfish and none of their own progeny!

Many cichlids expend enormous energy in altering their surroundings prior to reproduction. Elaborate sand nests, in the form of pits or cone-shaped mounds, are constructed by the males of some cichlid species for spawning. Some nest mounds are enormous, and require many days work by the male, moving sand one mouthful at a time. In certain species, lekking occurs: males build their nests in aggregations of various sizes. In Lake Malawi, male *Copadichromis eucinostomus* come together in groups as large as 50,000 individuals, stretched over several miles of sand, each guarding a cone-shaped nest. In Lake Tanganyika, numerous species from the tribe Lamprologini take advantage of abundant snail shells on the lake bottom as places of refuge and spawning sites. *Neolamprologus callipterus*, a haremic species, is noteworthy in that the males are dramatically larger than the females (as much



Some catfish eggs have evolved to look like cichlid eggs, so when a female cichlid (*Tropheus moorii*) collects her own eggs in her mouth, she inadvertantly collects some catfish eggs and raises them too. When the catfish eggs hatch, the young catfish eat the cichlid eggs. (Illustration by Michelle Meneghini)

Male rift lake cichlids have spots on their anal fins. When a female swims around collecting her eggs in her mouth after releasing them to be fertilized (1), she often mistakes the spots on the male's fin to be eggs. She bites the anal fin (2), and the eggs in her mouth are then fertilized. (Illustration by John Megahan)

30 times by weight), and only females occupy shells during spawning. Selection seems to maintain this size dimorphism because males need to be large enough to carry shells to their territories, while females need to be small enough to spawn inside the shells.

Conservation status

Although none of the surfperches are listed by the IUCN, hundreds of cichlid species are either extinct or in great peril. There are 133 cichlids on the IUCN Red List, 44 of which are listed as Extinct and five of which are listed as Extinct in the Wild. Of the 37 Critically Endangered cichlids, all are from Africa or Madagascar, and most are from either Lake Barombi Mbo in Cameroon or the East African lakes Victoria, Nabugabo, Kanyaboli, and Nawampasa. Humans are responsible for the plights of these fishes, which have declined due to the introduction of exotic species, pollution from industrial sources and sewage, sedimentation related to deforestation, and overfishing. The story of Lake Victoria is emblematic in this regard, as hundreds of species have been affected by the extensive degradation of the lake's ecosystem, and thus is considered here in some detail.

Gill nets were introduced to fishermen on Lake Victoria in 1905 to catch the endemic tilapiine cichlids *Oreochromis esculentus* and *Oreochromis variabilis*. Increasing fishing activity, aided by gill nets, quickly led to declines in catches of numerous species, including the tilapiines, catfishes, and lungfishes. By the 1950s, endemic tilapia had been all but wiped out, so the Nile perch (*Lates niloticus*) and four nonnative

tilapiine species were introduced: *Tilapia zilii*, *T. melanopleura*, *Oreochromis niloticus*, and *O. leucostictus*. Gill-net fisheries had since shifted to endemic catfishes, characins, cyprinids, and mormyrids, and as those stocks declined, fishermen were forced by the 1970s to shift their focus toward the abundant haplochromine cichlids and the pelagic cyprinid *Rastrineobola argentea*. Beach seines, which had been introduced to the region during the 1960s, exacerbated the problem of overfishing by disrupting the littoral spawning nests of tilapiine and haplochromine cichlids. Soon after a haplochromine trawl fishery was established in Tanzania, and a factory was built to convert the catch into chicken feed, the haplochromine fishery began its precipitous collapse. This was in the late 1970s, and was coincident with a population explosion of the much-maligned Nile perch. Lake Victoria fisheries were on the verge of total collapse, but were revitalized by the now-abundant Nile perch, supplemented by *Rastrineobola* and *Oreochromis niloticus*.

Small, bony haplochromines were not valued highly by local fishers, so creative schemes were concocted for utilizing them. Early on, it was suggested that haplochromines could be trawled and used as manure; later efforts at canning haplochromines as fish meal for livestock were hampered by the fact that the can was worth more than its contents. In areas where haplochromine trawling was implemented, however, populations declined dramatically. Their biology helps to explain why. Haplochromines are mouth brooders, and females produce a relatively small number of eggs. As narrow specialists with low-standing stocks and a low reproductive potential, they are peculiarly susceptible to collapse when nonselective fishing methods like trawling are used.

Although numerous factors, including overharvesting, appear to have precipitated the collapse of the haplochromine fishery, strong evidence implicates the Nile perch. In Mwanza Gulf, which was continuously surveyed during the 1980s, the Nile perch boom documented at the beginning of the decade was immediately followed by the total collapse of open-water haplochromine stocks. Haplochromines were selectively eaten until they were exhausted. Once Nile perch had colonized a part of the lake, the larger and less common haplochromine species were first to disappear there, especially those species with the most habitat overlap with Nile perch.

Another factor that has played a significant role in haplochromine cichlid collapse is eutrophication. The causes of Lake Victoria's eutrophication are numerous: deforestation, urban and industrial development around the shore, a rise in lake level, and even positive feedback from post haplochromine collapse food-web alterations (many haplochromines were specialized phytoplankton feeders and kept blooms in check). Since 1960, the lake's primary productivity has more than doubled, and more than half the bottom area of the lake is now devoid of oxygen below 98 ft (30 m). Drinking water for the human population on the lake's shores is now threatened by toxic blue-green algae blooms. In addition, the fact that large *Lates* cannot be sun dried like haplochromines, but instead require smoking over a wood fire, has accelerated deforestation and sedimentation in the basin, as the Nile perch fishery has expanded.

Eutrophication further threatens Lake Victoria's haplochromines in a very unexpected way. In a 1997 paper, Seehausen and collaborators argued that the decreased water transparency brought about by eutrophication has caused rock-dwelling cichlid declines by eroding between-species mating barriers. They point out that among the African Great Lake basins, only those lakes with clear water have given rise to cichlid species flocks. The sympatric haplochromine cichlids of Lake Victoria lack postmating reproductive barriers among closely related species, and have historically avoided hybridization through mate choice; this barrier is now breaking down as turbidity prevents females from recognizing males of their own species. Males of similar species are always manifestly distinct in coloration, and in experiments with monochromatic light, females lose their ability to discern conspecifics. Within different regions of the lake, *Haplochromis* color morphs behave as distinct species where the water is clear, and blend into homogenous hybrid populations where the water is cloudy.

Significance to humans

Both cichlids and surfperches are sought after by humans as sources of food. Tilapiine cichlids are easy to culture artificially, and so have been introduced around the world in fish-farming ventures. They supply an important source of protein to many human populations. However, exotic tilapiines have also adversely affected native fish populations in regions where they have been introduced by humans. Cichlids are enormously popular in the aquarium trade, and help support local economies in parts of the Americas and Africa through revenues from wild-caught fish exports. Numerous strains of certain species are also cultivated in captivity.

1. Worm cichlid (*Teleogramma gracile*); 2. *Paralabidochromis chilotes*; 3. Trout cichlid (*Champsochromis caeruleus*); 4. Millet (*Crenicichla alta*); 5. Agassiz's dwarf cichlid (*Apistogramma agassizii*); 6. Freshwater angelfish (*Pterophyllum scalare*); 7. Blunthead cichlid (*Tropheus moorii*). (Illustration by Barbara Duperron)

1. Rainbow seaperch (*Hypsurus caryi*); 2. Ngege (*Oreochromis esculentus*); 3. Trondo mainty (*Ptychochromoides betsileanus*); 4. Giant cichlid (*Boulengerochromis microlepis*); 5. Blue discus (*Symphysodon aequifasciata*); 6. Speckled pavon (*Cichla temensis*); 7. *Lepidiolamprologus kendalli*. (Illustration by Barbara Duperron)

Species accounts

Agassiz's dwarf cichlid
Apistogramma agassizii

FAMILY
Cichlidae

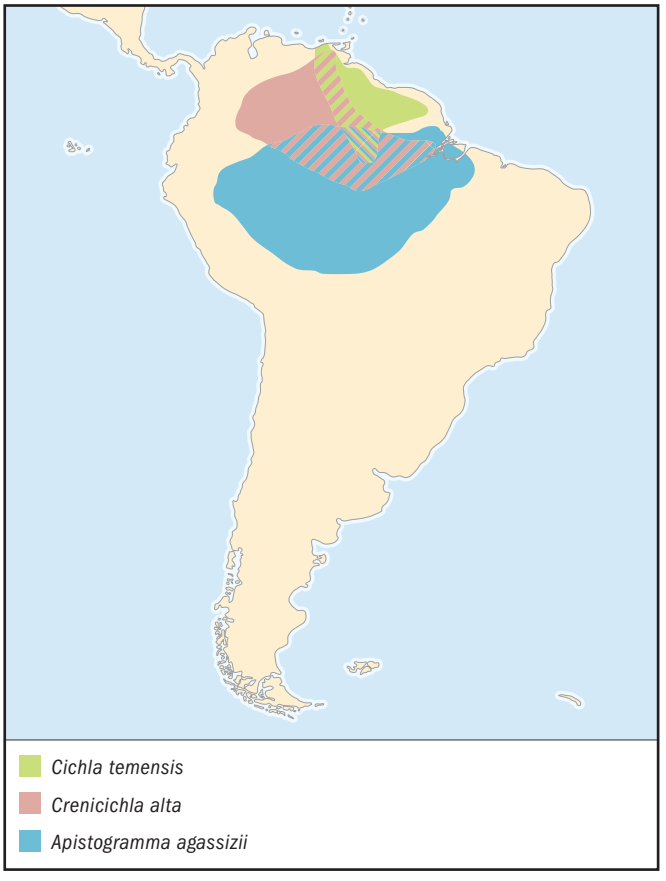
TAXONOMY
Geophagus (Mesops) agassizii Steindachner, 1875, Curupira, Codajas, Rio Poti de Sao Joao, Lago Maximo, and Lago Manacapuru, Brazil.

OTHER COMMON NAMES
German: Agassiz Zwergbuntbarsch.

PHYSICAL CHARACTERISTICS
Maximum length 2 in (5 cm). Dorsal and anal fins somewhat elongate, caudal fin spade shaped. Head somewhat rounded. Female coloration is lemon yellow; males brilliantly colored with yellows and blues anteriorly, a dark midlateral band, and red, black, and white bands on posterior fins.

DISTRIBUTION
Amazon basin along the Amazon River from Peru to the Capim River in Brazil.

HABITAT
Clear, black, and whitewater rivers.



BEHAVIOR
Males exhibit ritualized behaviors in defense of their territories; females in the harem of a single male compete for his attention.

FEEDING ECOLOGY AND DIET
Feeds on aquatic macroinvertebrates.

REPRODUCTIVE BIOLOGY
Eggs laid in caves, or in flowerpots in aquaria; they hatch in about four days. Practices harem polygyny.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Owing to its brilliant colors and peaceable demeanor, this fish is popular in the aquarium trade. ◆

Giant cichlid
Boulengerochromis microlepis

FAMILY
Cichlidae

TAXONOMY
Tilapia microlepis Boulenger, 1899, Lake Tanganyika at Moliro, Democratic Republic of the Congo, Africa.

OTHER COMMON NAMES
English: Yellowbelly cichlid; German: Riesenbuntbarsch; Swahili: Kuhe.

PHYSICAL CHARACTERISTICS
Maximum length 25.6 in (65 cm); largest African cichlid. Background color yellowish, with numerous dark but faint vertical bars. Four dark blotches along middle of flanks. Caudal fin lunate.

DISTRIBUTION
Widely distributed in Lake Tanganyika, East Africa.

HABITAT
Deeper water over sand as well as open water, enters shallower waters to breed.

BEHAVIOR
Cruises open waters in pursuit of schools of small fishes.

FEEDING ECOLOGY AND DIET
Feeds on smaller fishes.

REPRODUCTIVE BIOLOGY
Substrate spawners, uses rocks or abandoned nests of other cichlids to deposit eggs. Both parents aggressively guard fry, have even been known to attack scuba divers who approached too close to a nest. Lays 5,000–12,000 eggs during spawning; eggs hatch in about three days. Some evidence suggests that pairs do not feed again after spawning, and spawn only once in a lifetime.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular sport fishes with excellent tasting flesh. ◆

Trout cichlid
Champsochromis caeruleus

FAMILY
Cichlidae

TAXONOMY
Paratilapia caerulea Boulenger, 1908, Lake Malawi.

OTHER COMMON NAMES
German: Forellen-Cichlide; Nyanja: Ndunduma.

PHYSICAL CHARACTERISTICS
Maximum length 12.6 in (32 cm). Large, predatory cichlid with slender body. Dorsal, anal, and pelvic fins somewhat elongate in adults. Immature males and females silver gray, with dark band running obliquely along uppermost part of body. Breeding males acquire brilliant greenish blue coloration, and edges of the dorsal and anal fins become orange.

DISTRIBUTION
Widely distributed in Lake Malawi, East Africa.

HABITAT
Inshore waters to depths of 180 ft (55 m).

BEHAVIOR
Juveniles school together, but adults usually cruise solitarily.

FEEDING ECOLOGY AND DIET
Feeds on smaller fishes.

REPRODUCTIVE BIOLOGY
Mouth brooder. Male forms a pit over sandy substrate. Female lays eggs in the pit and then collects them; eggs are fertilized in the female's mouth.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Locals occasionally catch these fish using baited hooks. ◆

Speckled pavon
Cichla temensis

FAMILY
Cichlidae

TAXONOMY
Cichla temensis Humboldt, 1821, Rio Temi, Venezuela.

OTHER COMMON NAMES
English: Peacock bass, tucunare; German: Humboldtcichlide; Spanish: Pavón.

PHYSICAL CHARACTERISTICS
Maximum length 39 in (99 cm); perhaps the world's largest cichlid. Elongate with large head, has superficial appearance of a bass. Spinous and soft-rayed dorsal fin subdivided. Background color yellow green to tan, with three dark vertical bars and a series of horizontal rows of cream-colored spots. Ocellus on caudal fin; red on pelvic, anal, and lower lobe of caudal fins. Males acquire nuchal hump during spawning.

DISTRIBUTION
Amazon Basin in Rio Negro and Rio Uatumã systems; Orinoco basin in Venezuela and Colombia; introduced in Florida and Texas.

HABITAT
Along banks of main river channels over sand and rocks, and in deeper inshore waters of lagoons.

BEHAVIOR
Voracious predators; in aquaria, they ignore any fishes that are too large to swallow.

FEEDING ECOLOGY AND DIET
Feeds on other fishes.

REPRODUCTIVE BIOLOGY
Monogamous substrate spawners. Both parents care for eggs and young. Eggs may number up to 4,000, and are laid on logs, rocks, or in excavated pits.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular sport and food fishes. Also found in the aquarium trade. ◆

Millet
Crenicichla alta

FAMILY
Cichlidae

TAXONOMY
Crenicichla alta Eigenmann, 1912, Gluck Island, Guyana.

OTHER COMMON NAMES
English: Spangled pike cichlid.

PHYSICAL CHARACTERISTICS
Maximum length 6.3 in (16 cm). Elongate, pikelike, with pointed snout. Lower jaw extends beyond upper. Color grayish on flanks, with dark stripe running from tip of snout to caudal fin. Abdomen rose colored, cheek yellow. Ocelli on caudal fin and shoulder; dorsal, anal, and caudal fins have black and white edges.

DISTRIBUTION
Rio Branco River drainage, Brazil, and Essequibo River drainage, Guyana.

HABITAT
Rivers and streams.

BEHAVIOR
Juveniles school together, adults are solitary.

FEEDING ECOLOGY AND DIET
Feeds on smaller fishes.

REPRODUCTIVE BIOLOGY
Spawns in caves, which males dig into the bank. Both parents care for eggs and fry.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally found in the aquarium trade. ◆

No common name
Paralabidochromis chilotes

FAMILY
Cichlidae

TAXONOMY
Paratilapia chilotes Boulenger, 1911, Jinja, Ripon Falls, Uganda.

OTHER COMMON NAMES
German: Viktoria-Wulstlippen-Maulbrüter.

PHYSICAL CHARACTERISTICS
Maximum length 5.8 in (14.8 cm). Elongate, unicuspid, forward-directed teeth used like forceps to capture insect larvae. Lips dramatically swollen and enlarged. Color pattern varies geographically; most populations are yellow-gray over most of body. Males with green and blue on flanks, orange on dorsal, anal, and caudal fins, and chest. Females sometimes exhibit piebald coloration.

DISTRIBUTION
Lake Victoria, East Africa.

HABITAT
Sheltered inshore waters with rocky bottom to 55.8 ft (17 m) depth

BEHAVIOR
In aquaria, observed digging under overhanging rocks for prey. Presses large lips against cracks in rocks when feeding. Not as territorial as many other haplochromines.

FEEDING ECOLOGY AND DIET
Feeds mainly on mayfly larvae, though also eats larvae of Trichoptera (caddisflies) and Diptera (true flies).

REPRODUCTIVE BIOLOGY
Mouth-brooder.

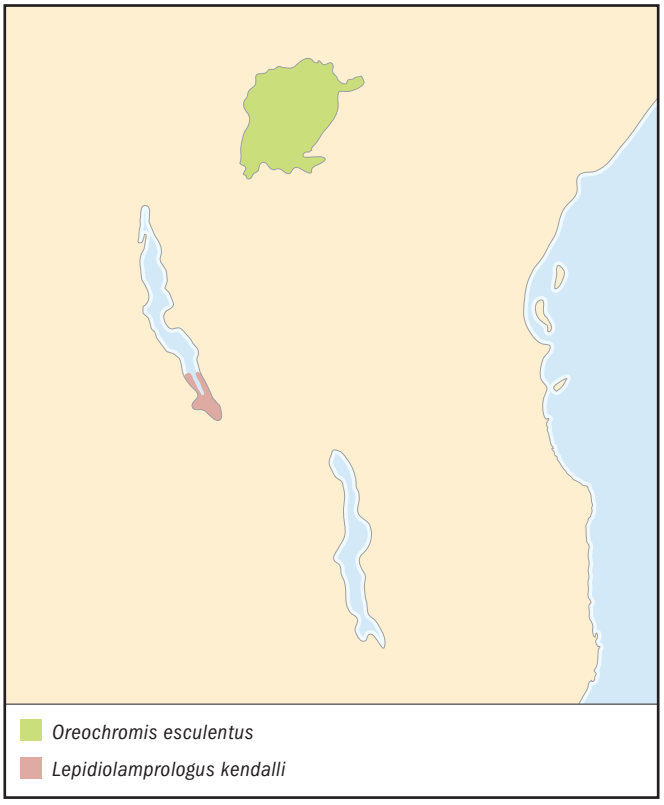
CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Found in the aquarium trade; one of the Lake Victoria haplochromines that has survived the Nile perch boom and other perturbations that have befallen the lake. ◆

No common name
Lepidiolamprologus kendalli

FAMILY
Cichlidae

TAXONOMY
Lamprologus kendalli Poll and Stewart, 1977, Lake Tanganyika, northwest of Mutondwe Island, Zambia.



OTHER COMMON NAMES
German: Kendalls Tanganjikasee-Buntbarsch.

PHYSICAL CHARACTERISTICS
Maximum length 6.3 in (16 cm). Elongate and torpedo shaped. Dark background color, with white blotching on head and fins, and white blotches forming several almost continuous horizontal bands on flanks. Hints of blue on face, pectoral fins yellowish.

DISTRIBUTION
Southern part of Lake Tanganyika, East Africa.

HABITAT
Shallow rocky areas as well as deeper waters, up to about 148 ft (45 m).

BEHAVIOR
Adults are solitary, and cover large distances in search or prey.

FEEDING ECOLOGY AND DIET
Feeds on other fishes.

REPRODUCTIVE BIOLOGY
Substrate spawner. Females may release up to 500 eggs. In the wild, spawns at a depth of 148 ft (45 m) over a rocky bottom covered with thick sediment.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Exported for the aquarium trade. ◆

Ngege
Oreochromis esculentus

FAMILY
Cichlidae

TAXONOMY
Tilapia esculenta Graham, 1928, Kenya, Lake Victoria.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum length 19.7 in (50 cm). Relatively deep bodied, with small head. Color olive-brown to dull green, becoming whitish ventrally. Breeding males become red dorsally and black ventrally, except that dorsal fin is also black.

DISTRIBUTION
Lake Victoria, Lake Nabugabo, Lake Kioga, Lake Kwania, the Victoria Nile above Murchison falls, and the Malawa River. Also Lake Gangu, west of Lake Victoria. Introduced into Tanzanian and Ugandan reservoirs.

HABITAT
Inshore waters with aquatic vegetation when young, move into open water as adults, to depths of 164 ft (50 m). Found over muddy bottoms.

BEHAVIOR
Adults school together in open water, following plankton blooms.

FEEDING ECOLOGY AND DIET
Plankton feeder, follows diatom blooms in lakes. Secretes mucous in the mouth that helps trap plankton, forming a bolus for swallowing.

REPRODUCTIVE BIOLOGY
Mouth brooder; fertilization takes place in female's mouth. Spawns year round. Males aggregate around spawning grounds, where they occupy basin-shaped nests and defend a small territory. Once eggs are fertilized, females move to weed beds with the brood.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Historically an important food fishery in Lake Victoria, but was overfished to the point of commercial extinction in the lake, where introduced tilapiines now predominate. ◆

Freshwater angelfish
Pterophyllum scalare

FAMILY
Cichlidae

TAXONOMY
Zeus scalaris Lichtenstein, 1823, Brazil.

OTHER COMMON NAMES
English: Black angelfish, longfin angelfish, veil angelfish; French: Poisson ange, scalaire; German: Dumerils, Perlscalar, Segelflosser; Spanish: Pez angel.

PHYSICAL CHARACTERISTICS
Maximum length 3 in (7.5 cm). Very deep bodied and laterally compressed, with diamond-shaped body. Dorsal, anal, and

pelvic fins very elongate. Adults silvery in color with four dark vertical bars; juveniles have seven bars.

DISTRIBUTION
Widely distributed in the Amazon basin; found in Peru, Colombia, and Brazil in the Ucayali, Solimões and Amazonas Rivers. Also in the rivers of Amapá, Brazil, the Oyapock in French Guiana, and the Essequibo River in Guyana.

HABITAT
Lakes, swamps, and flooded forests with dense aquatic vegetation and minimal current.

BEHAVIOR
Peaceable, gregarious fishes that take refuge in aquatic vegetation.

FEEDING ECOLOGY AND DIET
Feeds mainly on benthic crustaceans, including shrimps, prawns, and *Artemia nauplii.*

REPRODUCTIVE BIOLOGY
Forms monogamous pairs. Female spawns on thick plant leaves, and both parents care for eggs and young. Male and female nibble at eggs to release wrigglers about a day and a half after spawning, and may move brood to a pit in the substrate.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Exceedingly popular in the aquarium trade, with millions of specimens sold every year; numerous color and fin varieties have been selectively bred. ◆

Trondo mainty
Ptychochromoides betsileanus

FAMILY
Cichlidae

TAXONOMY
Tilapia betsileana Boulenger, 1899, Betsileo, Madagascar.

OTHER COMMON NAMES
French: Marahrely à bosse.

PHYSICAL CHARACTERISTICS
Maximum length 9.4 in (24 cm). A fairly deep-bodied, robust fish, usually with a well-developed occipital hump. Color black or dark gray, without stripes or bars. Females appear to be speckled and lighter in color, with white blotches on the cheek.

DISTRIBUTION
Central highlands of Madagascar, from the Betsileo region to Lake Itasy in the Merina district.

HABITAT
Cool, clear, well-oxygenated waters. In rivers, often found near rapids and waterfalls; found in deep waters with rocky substrate in Lake Itasy.

BEHAVIOR
Very little is known, except that the species seeks out riffles with rocky substrate.

FEEDING ECOLOGY AND DIET
Omnivorous, feeds on shrimp, aquatic insect larvae, aquatic plants, and phytoplankton.

REPRODUCTIVE BIOLOGY
Spawns on substrate; both parents care for fry for an extended period. Reproduces from October to early November. Females lay many hundreds of eggs, preferably on large rocks.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN.

SIGNIFICANCE TO HUMANS
Human encroachment has caused the extinction of this species in the northern part of its range, and the remaining populations are decimated. ◆

Blue discus
Symphysodon aequifasciata

FAMILY
Cichlidae

TAXONOMY
Symphysodon discus aequifasciata Pellegrin, 1904, Teffé and Santarém, Brazil.

OTHER COMMON NAMES
English: Brown discus, green discus; German: Blauer Diskus, Grüner Diskus, Scheibenbarsch; Spanish: Disco azul, pez disco.

PHYSICAL CHARACTERISTICS
Maximum length 5.5 in (14 cm). Extremely laterally compressed, almost perfectly round, dinner-plate shaped. Background yellow-green to tan, with brilliant undulating streaks of turquoise blue and numerous dark vertical bands running in parallel.

DISTRIBUTION
Amazon basin from the Rio Putumayo in Colombia and Peru to the Rio Tocantins in Brazil.

HABITAT
Calm waters in and around rock crevices, roots, and aquatic vegetation.

BEHAVIOR
Rather shy, schooling fish, most comfortable in or near tangles of submerged roots and branches or rock crevices. Becomes somewhat territorial during spawning.

FEEDING ECOLOGY AND DIET
Feeds on insects and insect larvae, as well as zooplankton.

REPRODUCTIVE BIOLOGY
Forms monogamous pairs in which both parents care for the young. Females lay clutches of about 100 eggs, which hatch in roughly 60 hours, on branches or sturdy leaves. Within 4–5 days, fry become mobile and begin feeding on mucous secreted from flanks of the parents, showing preference for the male. In captivity, this mode of feeding can last as long as 8 weeks, although other foods supplement the habit.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Extremely popular in the aquarium trade; many captive-bred strains exist. ◆

Worm cichlid
Teleogramma gracile

FAMILY
Cichlidae

TAXONOMY
Teleogramma gracile Boulenger, 1899, Matadi, Democratic Republic of Congo, Africa.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Maximum length 3.2 in (8 cm). Very elongate, cigar shaped; teeth small and unicuspid, with a few enlarged canines anteriorly. Uncharacteristically for cichlids, has single, continuous row of lateral line scales, instead of upper and lower divisions. Brownish in color, with thin red margin to dorsal fin and upper lobe of caudal fin. Females exhibit broad black margin above red patch in upper lobe of caudal fin.

DISTRIBUTION
Lower Congo River rapids.

HABITAT
Turbid, fast-flowing waters in lower Congo.

BEHAVIOR
Displays extreme territoriality toward conspecifics in aquaria. Hides under rocks and in caves.

FEEDING ECOLOGY AND DIET
Feeds on aquatic macroinvertebrates.

REPRODUCTIVE BIOLOGY
Spawns in caves, female tends to eggs. Polygynous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Very rarely exported for the aquarium trade. ◆

Blunthead cichlid
Tropheus moorii

FAMILY
Cichlidae

TAXONOMY
Tropheus moorii Boulenger, 1898, Kinyamkolo, Lake Tanganyika, Africa.

OTHER COMMON NAMES
English: Brabant cichlid, moorii; German: Brabantbuntbarsch.

PHYSICAL CHARACTERISTICS
Maximum length 5.7 in (14.5 cm). Moderately deep bodied, with blunt head and snout and down-turned mouth. Bicuspid outer row of teeth, tightly spaced. Exhibits wide range of geographical color variation, with populations ranging from uniformly dark brown with vertical bars to brilliant yellow with red fins.

DISTRIBUTION
Patchily distributed along the southern shores of Lake Tanganyika, Africa.

HABITAT
Shallow inshore waters with rocky substrate.

BEHAVIOR
Sometimes forms large schools composed of hundreds of individuals, which patrol rocky habitats in search of algal mats. Males are territorial, and will defend feeding territories.

FEEDING ECOLOGY AND DIET
Tears strands of algae from rocks.

REPRODUCTIVE BIOLOGY
Maternal mouth brooder; after laying 5–17 eggs, female collects them in her mouth and positions herself near male's genital area to receive sperm. Fertilization takes place in female's mouth. Eggs hatch after about four weeks. Females continue to guard offspring for a few days after they are first released from the mouth.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Popular in the aquarium trade. ◆

Rainbow seaperch
Hypsurus caryi

FAMILY
Embiotocidae

TAXONOMY
Embiotoca caryi Agassiz, 1853, San Francisco Bay, California, United States.

OTHER COMMON NAMES
English: Rainbow surfperch; Spanish: Perca.

PHYSICAL CHARACTERISTICS
Maximum length 11.8 in (30 cm). Deep bodied and laterally compressed, lateral line scales uninterrupted. Red and blue stripes on body and about 10 reddish brown bars on upper part of flanks. Pelvic and anal fins reddish orange with blue edges.

DISTRIBUTION
Pacific coast from Cape Mendocino, California, United States, to Isla San Martin, Baja California.

HABITAT
Around rocky shores, reefs, piers, and kelp beds, to depths of 132 ft (40.2 m).

BEHAVIOR
In the fall, gathers in large aggregations prior to breeding; females move into shallow coastal waters to give birth the following summer. Sometimes function as cleaner for other fishes by picking off parasites.

FEEDING ECOLOGY AND DIET
Feeds during day; eats mostly amphipods and copepods. Described as an oral winnower, meaning it takes mouthfuls of sand or turf, selectively removes food items, and spits out the remainder.

REPRODUCTIVE BIOLOGY
Viviparous; nutrient and gas exchange occurs between mother and the developing embryos. Females gravid from April until mid-September, and carry 9–22 young. Juveniles born at lengths of about 2.7 in (6 cm). Males develop swelling in tissues surrounding first anal fin spine during breeding, creating an intromittent (copulatory) organ used in internal fertilization. After mating, sperm are stored for several months in female's ovarian cavity prior to fertilization.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Minor commercial importance as food fishes. ◆

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Robert Schelly, MA

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Labroidei II

(Damselfishes, wrasses, parrotfishes, and rock whitings)

Class Actinopterygii
Order Perciformes
Suborder Labroidei
Number of families 4

Photo: Threespot dascyllus (*Dascyllus trimaculatus*) pair spawning over coral rocks near the Florida Islands, Solomon Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The four families in this grouping are part of the suborder Labroidei. The families are: Labridae (the wrasses); Scaridae (the parrotfishes); Pomacentridae (the damselfishes); and Odacidae (the rock whitings, or butterfishes, of western Pacific waters; the butterfishes of North America represent a different family).

The family Labridae is a large one, with approximately 500 species in 60 genera. The next largest of the four families is the Pomacentridae, with more than 320 species in 28 genera, followed by the Scaridae, with 83 species in 9 genera, and finally the Odacidae, with 12 species in 4 genera.

The taxonomy of these four families is under dispute, and several studies are under way to iron out the relationships. In fact, some taxonomists feel the scarids and odacids, which are believed to have evolved from labrids, should actually be listed as subfamilies within Labridae. Other researchers have focused their work on the evolutionary relationships among genera within families. As the genetic makeup of individual species becomes a more prominent tool in defining evolutionary relationships, there is little doubt that some shaking looms ahead for these branches of the tree of life.

Physical characteristics

This grouping of fishes is varied, but vibrant color is a trademark of many species in the four families, and has made wrasses and damselfishes the highlights of reef-diving excursions. In addition, the scarids, labrids, and odacids all share unusual pharyngeal modifications that serve as additional chewing surfaces to grind kelp, hard-shelled invertebrates, and other dietary items.

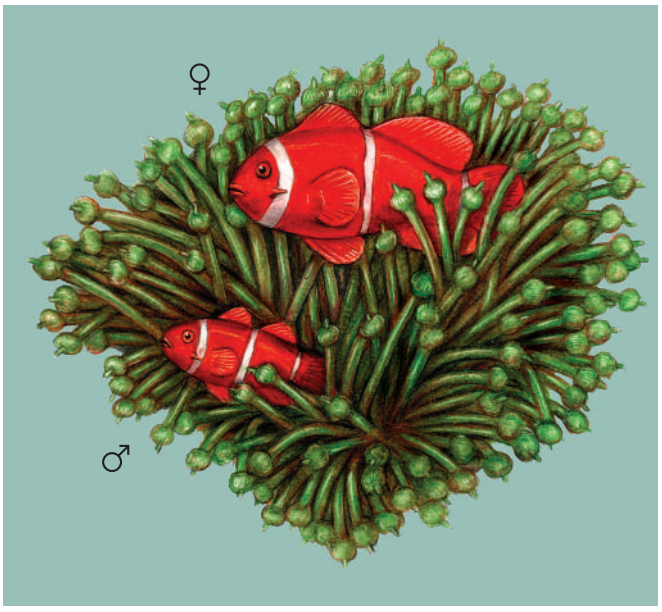
Generalizations can also be made about each of the four families. Most labrids, or wrasses, have gapped and outward-projecting teeth on protrusible upper and lower jaws. The dorsal fin typically has less than 15 spines; some have as many as 21 spines and 6–21 soft rays. The anal fin has 4–6 spines and 7–18 soft rays. Other than these characteristics, little else is noticeably uniform among this highly diverse family. Maximum adult size in the family ranges from about 2 in (5 cm) in a variety of species, to more than 8 ft (2.5 m) in the humphead wrasse (*Cheilinus undulatus*).

A brindlebass (*Epinephelus lanceoletus*) having its teeth cleaned by a bluestreak cleaner wrasse (*Labroides dimidiatus*). (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

The pomacentrids, or damselfishes, are characterized by a deep, compressed body; a small mouth with short canine teeth; a usually two-spined anal fin; one dorsal fin with spines numbering 8–17, and 10–18 rays; and a lack of teeth on the palate. Maximum adult size ranges from 1.6 in (4 cm) in some *Chromis* and *Chrysiptera* species, to over 12 in (30 cm) in the garibaldi (*Hypsypops rubicundus*) and giant damselfish (*Microspathodon dorsalis*).

Scarids, or parrotfishes, have a rather distinctive "parrot's beak" resulting from a fusion of the teeth and often fleshy lips. The dorsal fin has 9 spines and 10 soft rays, the anal fin has 3 spines and 9 soft rays, and the pectoral fin has one spine and 5 soft rays. Large scales are evident even from some distance.

The small Odacidae family is still quite diverse, and is occasionally described as being intermediate between the scarids and labrids. The jaw teeth are fused in a manner similar to the parrotfishes, but they have a different dorsal fin pattern, with 12–23 spines, compared to the 9 spines in scarids. Odacids, the rock whitings or butterfishes, have the more elongate body seen in many labrids, but do not have the protrusible jaws.



Mated pair of spine-cheek anemonefish moves among the tentacles of its host, the bubble tip anemone. (Illustration by Joseph E. Trumpey)

Distribution

Parrotfishes, wrasses, and damselfishes occupy mainly tropical, marine waters of the Atlantic, Pacific, and Indian Oceans, but some species, particularly wrasses, extend well into cooler waters, and a few damselfishes exist in estuaries and occasionally venture into fresh water. The rock whitings are found in the temperate, coastal waters of Australia and New Zealand.

Habitat

This group comprises primarily reef-associated fishes, although a few make their homes in the open sea. The reefs provide a source of refuge, as many of the species use the nooks and crannies in the coral as daytime hiding places from predators. A number of species also gain nourishment directly from the coral by nipping off polyps and grinding them with their pharyngeal jaws. Some species, particularly the juveniles, prefer the shallower, protected waters of lagoons and bays, and the adults of many reside in waters of steep, outer, reef slopes.

A threespot damselfish (*Stegastes planifrons*) in its nest amidst fire coral near Bonaire, Netherlands Antilles. (Photo by Charles V. Angelo/ Photo Researchers, Inc. Reproduced by permission.)

A number of parrotfishes live among beds of sea grass or in rocky reefs, and wrasses frequently require living coral reefs, but some do very well among dead coral. Damselfishes generally live in rocky and coral reefs, but individual species may prefer open water as deep as 300 ft (91 m) or more, or shallow habitats of as little as 12 ft (3.7 m) in either the open sea or in sheltered areas with calmer waters. Some species within these four families prefer very specific habitats. Anemonefishes (genera *Amphiprion* and *Premnis*), for example, may require the presence of a particular species of anemone.

Behavior

Two of the most well-known behaviors of this group of fishes involve that of certain damselfishes and their symbiotic relationship with large sea anemones, and that of parrotfishes, which produce a mucus "cocoon" that surrounds them while they sleep at night.

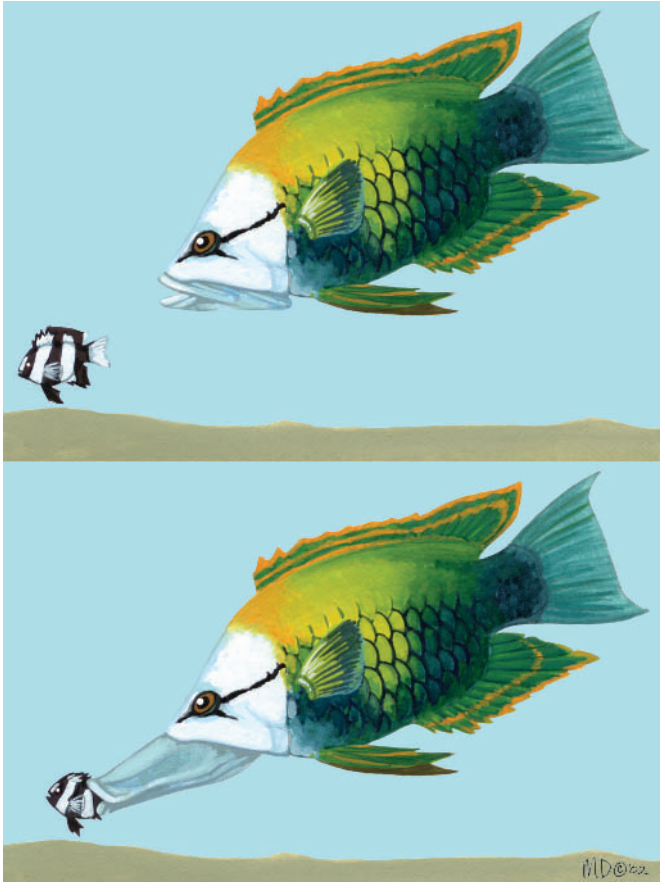
Known as anemonefishes, or clownfishes, the 30 damselfishes in the genera *Amphiprion* and *Premnas* move among and between the dangerous tentacles of the sea anemone, even sleeping within them. Stinging cells (nematocysts) on the surface of the tentacles normally sting and paralyze prey fish for easy consumption by the anemone. The anemonefishes, however, live peacefully among the anemones. Current consensus

is that a protective mucus coat on the anemonefish shields it from the sting of the tentacle. The relationship is symbiotic because both species gain from it. The anemonefish receives shelter from predators, while helping to maintain the health of the anemone by picking off organisms and detritus from its tentacles. The relationship is more important to the anemonefishes than to the anemones, because the fishes are unable to escape predation without the sanctuary of the anemone, but anemones can and do survive in the absence of the fishes.

Parrotfishes, on the other hand, have their own presumably protective behavior. At night, these diurnal animals prepare for sleep by generating a tube of mostly clear mucus that surrounds the body. The tube forms in about 30–60 minutes. There is some debate over whether cocoon formation is a behavioral trait or simply the result of normal mucus secretions that accumulate because the fish is stationary. Either way, the mucus tube appears to provide the fishes with some protection from predators by masking them, and perhaps by surrounding them with an unpleasant-tasting barrier.

Feeding ecology and diet

Herbivores and carnivores exist within this group, with the diet of many species comprising both plants and animals.

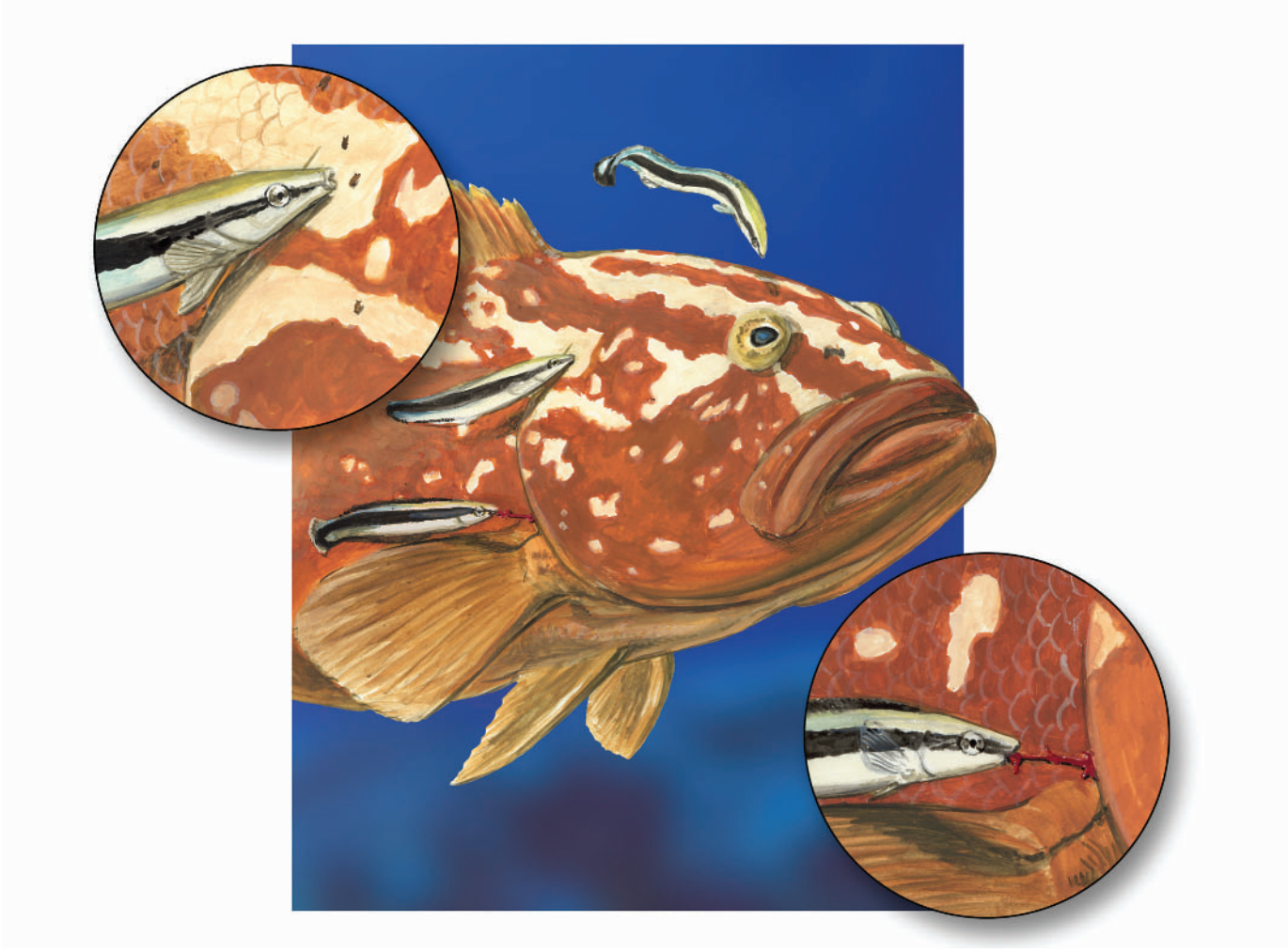


A slingjaw wrasse (*Epibulus insidiator*) sucks up prey, a humbug damsel (*Dascyllus aruanus*), through its long jaws. (Illustration by Marguette Dongvillo)

A parrotfish sleeps in a mucous cocoon in the reefs of Fiji. (Photo by Stuart Westmorland/CORBIS. Reproduced by permission.)

Feeding habits vary. The odacids are mainly herbivores, with a few dining on kelp, a coarse seaweed shunned by most other species. One study of the butterfish *Odax pullus* showed that this herbivorous odacid has an active symbiotic relationship with gut microbes that assists in the digestion of the plant matter. Several damselfishes hold feeding territories and even cultivate algal beds. Many scarids and odacids are herbivorous grazers, using their parrotlike beaks to scrape algae from rocks and coral, or to crush open a hard-shelled invertebrate, such as a mussel or sea urchin. A few even eat coral polyps. Some parrotfishes are so aggressive in their feeding habits that they are considered a cause of reef erosion, as they not only alter the reef, but also excrete a great deal of silty sediment that coats the reef structure. As a rule, species that dine on coral, mollusks, and other crunchy prey have more rounded teeth attuned to grinding. The teeth of species that favor softer dietary items are more pointed.

The wrasses are primarily carnivores, and generally choose from a variety of hard-shelled, invertebrate prey. Some, however, prefer that their food come to them, and take their diet of plankton from the water column. One of the most unusual feeding behaviors in this group is seen in the cleaner wrasses.



A cleaner wrasse cleans a fish (left inset). A cleaner mimic is a blenny that mimics the cleaner wrasse, but instead of cleaning the larger fish, it rips out a gill filament to eat (right inset). (Illustration by Brian Cressman)

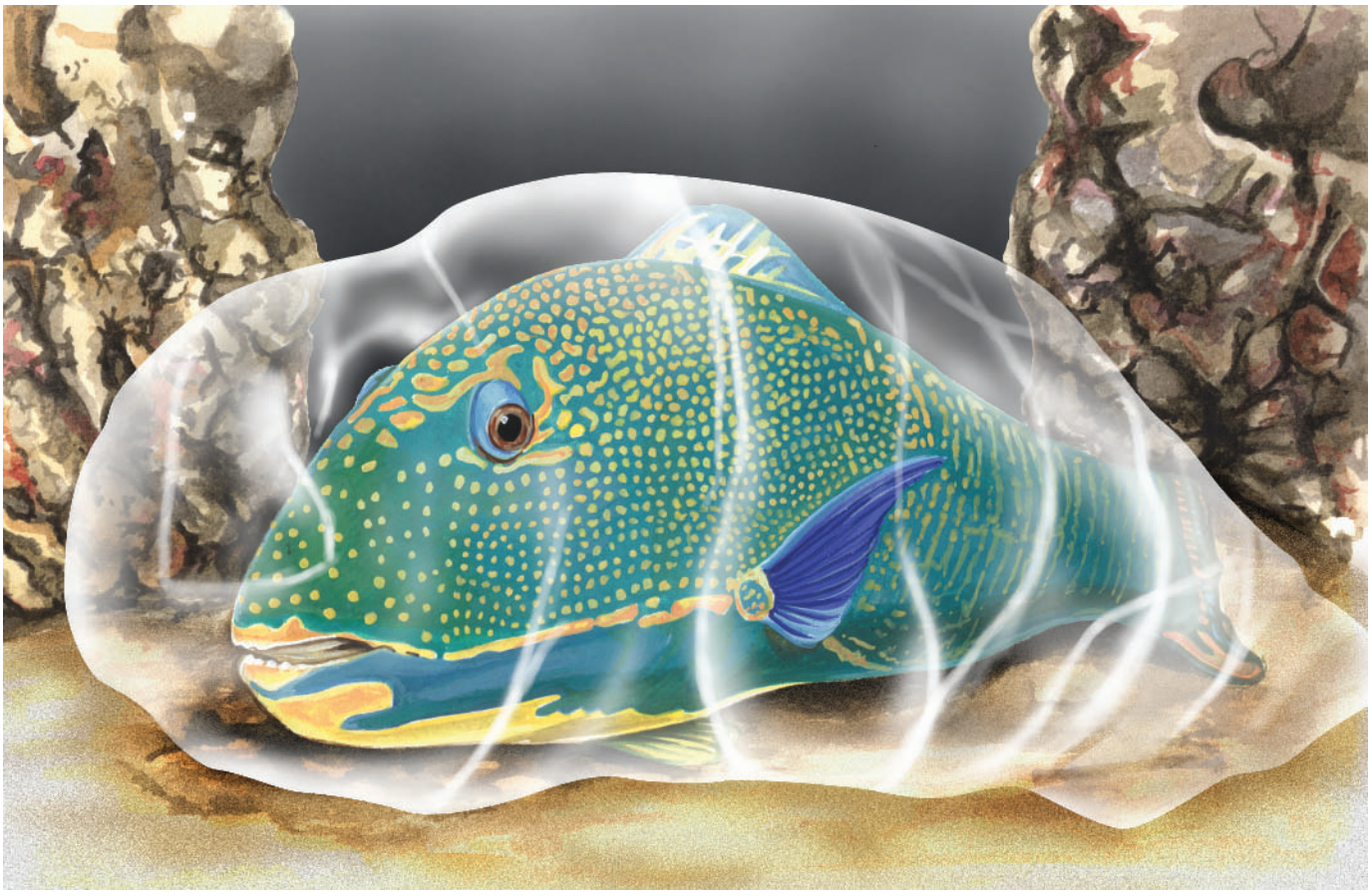
This group of small fishes in the genus *Labroides* have specific sites where they provide cleaning services to other fishes. Fishes come to these so-called cleaning stations, and announce their desire to be cleaned by exhibiting stereotyped behaviors through movements of their mouths or bodies. The cleaner wrasses strike a deal by responding with their own behaviors, including brushing the "client" with their fins, and the cleaning begins. The wrasses pick over the body, fins, and head of the client fish, and may even enter the gill chamber and mouth to remove crustacean ectoparasites, mucus, dead skin, dislodged scales, and other detritus. Both client and wrasse benefit from the arrangement: the cleaner is fed, and the client is cleaned.

Other wrasses also provide cleaning services, particularly juveniles of the genus *Thalassoma*. A study of Noronha wrasse (*T. noronhanum*) and a client fish, the piscivorous coney (*Cephalopholis fulva*) indicated that client fishes sometimes take advantage of the situation and eat the cleaner. In this study, scientists observed predation in two instances, both of which occurred when the wrasse was tending the coney away from its normal cleaning station.

Fishes in these four families may fall prey to larger bony fishes. The primary predators include larger serranids, synodontids, aulostomids, and members of other families.

Reproductive biology

Perhaps most notable characteristics of this group of fishes are the three separate color phases and sex reversal associated with many species. The typical three-phase lifestyle begins with a juvenile (immature) phase, then an adult initial phase, and finally the terminal phase. Each has a distinctive appearance that differs from species to species. In the bluehead wrasse (*Thalassoma bifasciatum*), for example, juveniles are bright yellow, initial-phase adults are yellow with black stripes, and terminal-phase males are deep blue with a green rear and midbody, and bold, black and white bands behind the head. The initial-phase adults in many species are almost all females, and in most cases, the few initial-phase males look the same as their female counterparts. The initial and terminal phases are usually so different that inexperienced divers



Detail of a parrotfish cocoon. (Illustration by Patricia Ferrer)

frequently assume they are two species. This three-phase lifestyle is characteristic of the wrasses and parrotfishes. Damselfishes typically shift gradually from a colorful juvenile pattern into a the more drab suit of an adult.

Along with the three color phases in the parrotfishes and wrasses, these two families engage in sex reversal. Here, the initial-phase adults usually are mostly female, often living in a small grouping, or harem. Each harem has one terminal-phase male, which mates with the adult females. The females form a hierarchy within the harem, with one dominant female followed by a second-ranking female, a third, and so on. If the male is removed from the group through predation or other means, the dominant female steps up to become, socially and physiologically, the terminal-phase male. The social change can occur in as little as a few hours. The physiological change, including the development of functional testes, may take a couple of weeks. The hierarchy among the females continues, with the second-ranking female moving into the position of dominant female, and the rest moving up a step in the hierarchy.

Initial-phase males are also capable of becoming the terminal-phase male, and this frequently occurs in non-haremic groups. In this reproductive arrangement, the terminal-phase males set up a territory where females may enter for one-on-one mating. When the terminal-phase male is removed, an initial-phase male or female may take his place. Another reproductive strategy is available for initial-phase males, which are sexually mature. Initial-phase males will form schools, and chase individual females as they make their way to a terminal male's territory, and "sneak-spawn" with them. Although sole paternity is out of the question for individual sneak-spawners, at least the initial-phase male can add his milt to the mix and perhaps fertilize a few eggs. Many of these fishes also engage in mass spawning, in which both terminal-phase and initial-phase males participate.

Damselfishes may not have the obvious phase differences, but they do have interesting reproductive behavior. As a group, these fishes are quite territorial of their mating sites and will mount vicious attacks on intruders, complete with rushes, grunts, and bites. The male typically clears a nest site, engages in ritualistic visual and tactile displays to attract a female, mates, and then cares for the eggs until they hatch, when the young are on their own. In an unusual twist, the marine damselfish (*Acanthochromis polyacanthus*) continues its care of the young for several months after hatching. Anemonefishes are noted because they reverse gender like the parrotfishes and wrasses, but in the opposite direction. In an anemone, this species exists in small groups with one large female, one large male, and several small, immature males. Should the large female be removed, the most-dominant immature male can develop to take her place.

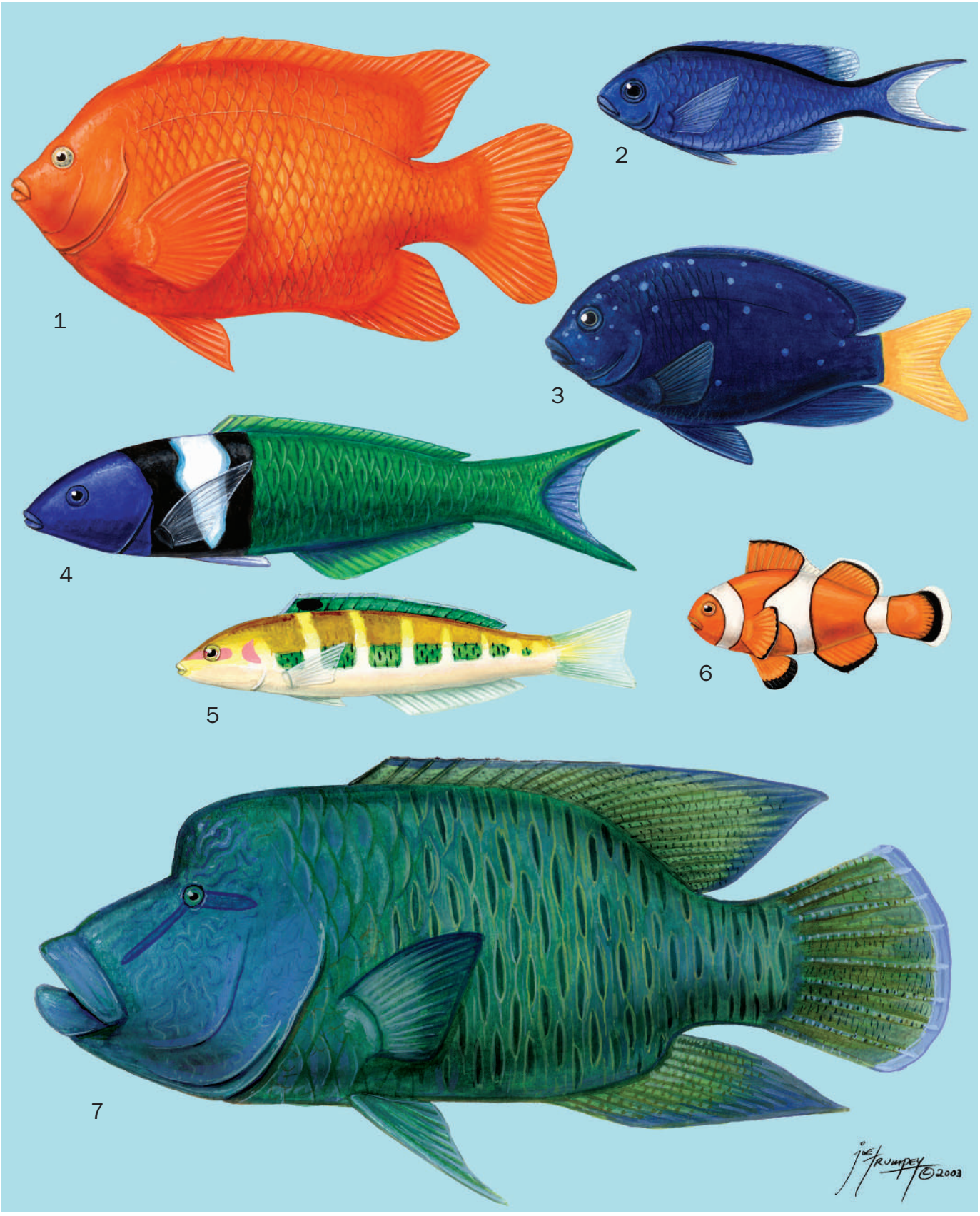
Little is known about reproduction in odacids overall, but the butterfish *O. pullus* does change sex from female to male and exists in small harems. Females lay their eggs directly into a plankton column.

Conservation status

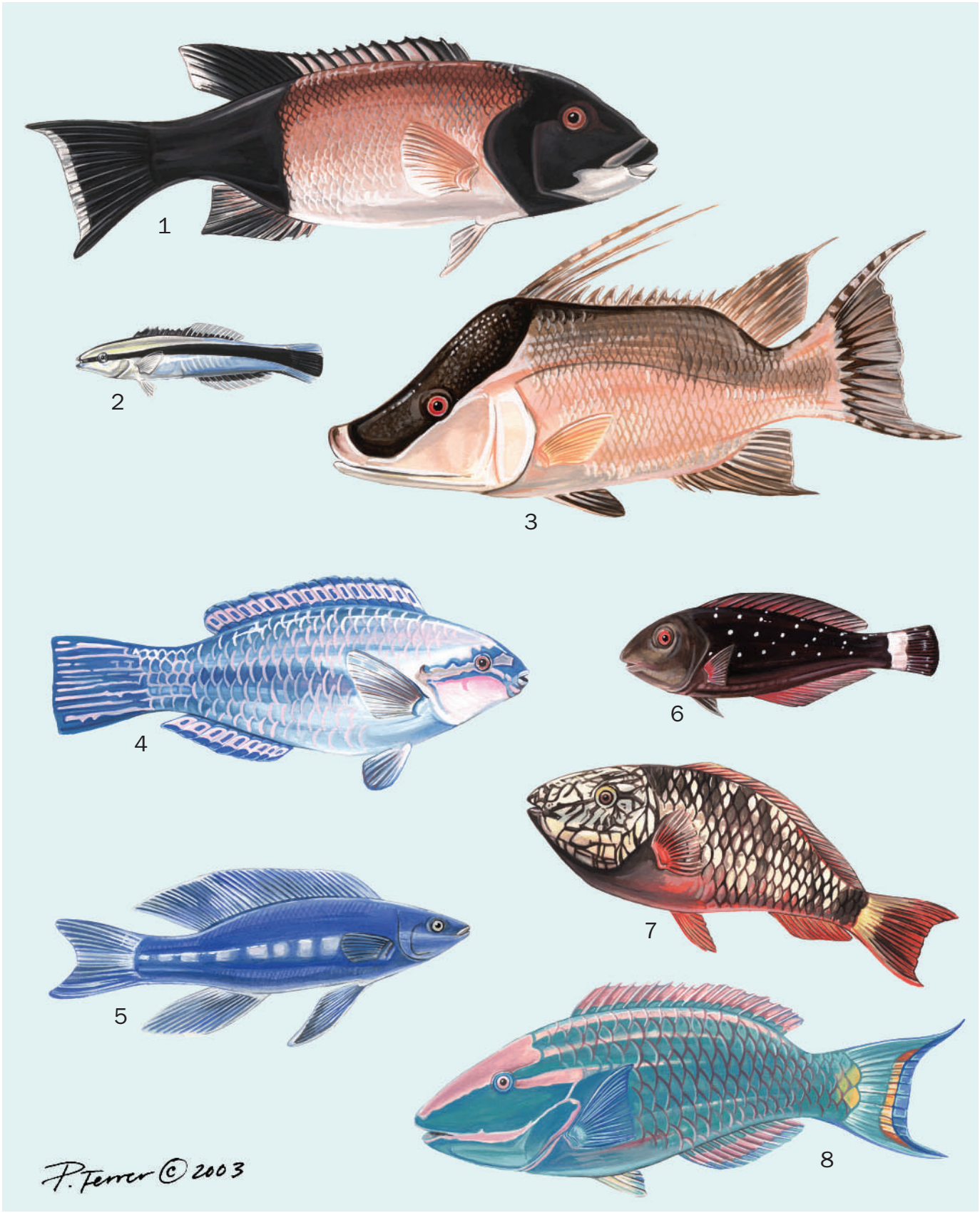
Eight species are included on the IUCN Red List, all of them categorized as Vulnerable. The eight species are: in the Pomacentridae, *Chromis sanctaehelenae*, *Stegastes sanctaehelenae*, and *S. sanctipauli*; in the Labridae, *Cheilinus undulatus*, *Lachnolaimus maximus*, *Thalassoma ascensionis*, and *Xyrichtys virens*; and in the Scaridae, *Scarus guacamaia*.

Significance to humans

Aesthetic, particularly to divers, and often popular in the aquarium trade. A few are minor commercial food fishes.



1. Garibaldi damselfish (*Hypsypops rubicundus*); 2. Blue chromis (*Chromis cyanea*); 3. Yellowtail damselfish (*Microspathodon chrysurus*) intermediate stage; 4. Bluehead adult (*Thalassoma bifasciatum*); 5. Bluehead (*Thalassoma bifasciatum*) intermediate stage; 6. Clown anemonefish (*Amphiprion ocellaris*); 7. Humphead wrasse (*Cheilinus undulatus*). (Illustration by Joseph E. Trumpey)



1. California sheephead (*Semicossyphus pulcher*); 2. Bluestreak cleaner wrasse (*Labroides dimidiatus*); 3. Hogfish (*Lachnolaimus maximus*); 4. Striped parrotfish (*Scarus iseri*); 5. Butterfish (*Odax pullus*); 6. Juvenile stoplight parrotfish (*Sparisoma viride*); 7. Initial phase of the stoplight parrotfish; 8. Terminal phase of the stoplight parrotfish. (Illustration by Patricia Ferrer)

Species accounts

Humphead wrasse
Cheilinus undulatus

FAMILY
Labridae

TAXONOMY
Cheilinus undulatus Rüppell, 1835, Jidda, Saudi Arabia, Red Sea.

OTHER COMMON NAMES
English: Maori wrasse, Napoleon wrasse; French: Napoléon; Spanish: Napoleón.

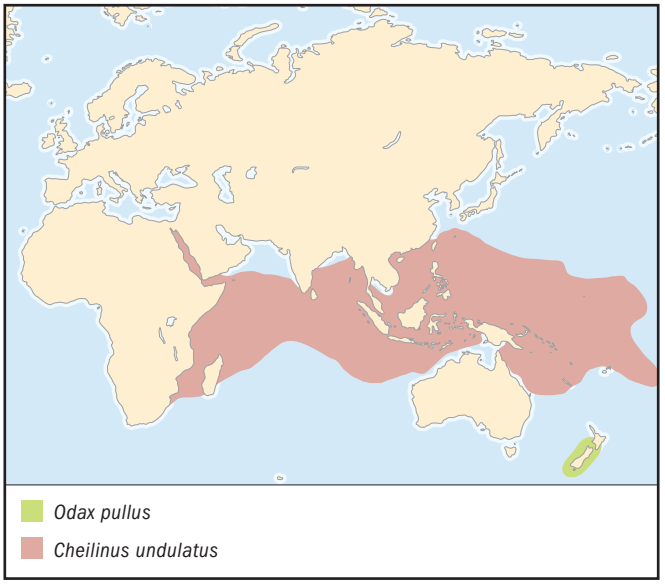
PHYSICAL CHARACTERISTICS
Length 5 ft (about 1.5 m), although a few have been recorded at more than 8.2 ft (2.5 m); one of the largest reef fishes. The large adult has distinctive hump on the top of the blue-fronted, small-eyed, thick-lipped head; rest of the body is yellowish green. Juveniles pale green, with horizontally placed spots or bar extending down the sides of the body.

DISTRIBUTION
Much of the Red Sea and Indian Ocean, east through Indonesia to Tuamotus, French Polynesia, and north to southern Japan.

HABITAT
Juveniles frequent sea grass beds and reef lagoons. Adults prefer deeper reef areas to 325 ft (100 m) deep.

BEHAVIOR
Shy, diurnal, remains among reef refuges at night. Usually solitary, but will sometimes live in pairs or in small groups.

FEEDING ECOLOGY AND DIET
Feeds during the day, primarily on mollusks, but also takes fishes, as well as other invertebrates such as brittle stars and sea urchins.



REPRODUCTIVE BIOLOGY
Both small and large spawning aggregations form, but fishes pair up for mating. No parental care. Sex reversal has been noted, in which females develop into mature males.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Commercial food fish whose intensive exploitation has led to concern for the survial of local populations of this species. Also popular aesthetically to divers. ◆

Bluestreak cleaner wrasse
Labroides dimidiatus

FAMILY
Labridae

TAXONOMY
Labroides dimidiatus Valenciennes, 1839, El Tûr, Sinai Coast, Egypt, Gulf of Suez; Mauritius.

OTHER COMMON NAMES
English: Bridled beauty, cleaner wrasse; French: Bande bleue, nettoyeur à poisson doctère, poisson nettoyeur commun.

PHYSICAL CHARACTERISTICS
Total length 4.5 in (11.5 cm). Adults mostly light blue, with long black stripe running along each side of body, widening as it approaches the tail. Juveniles black with blue dorsal stripe.

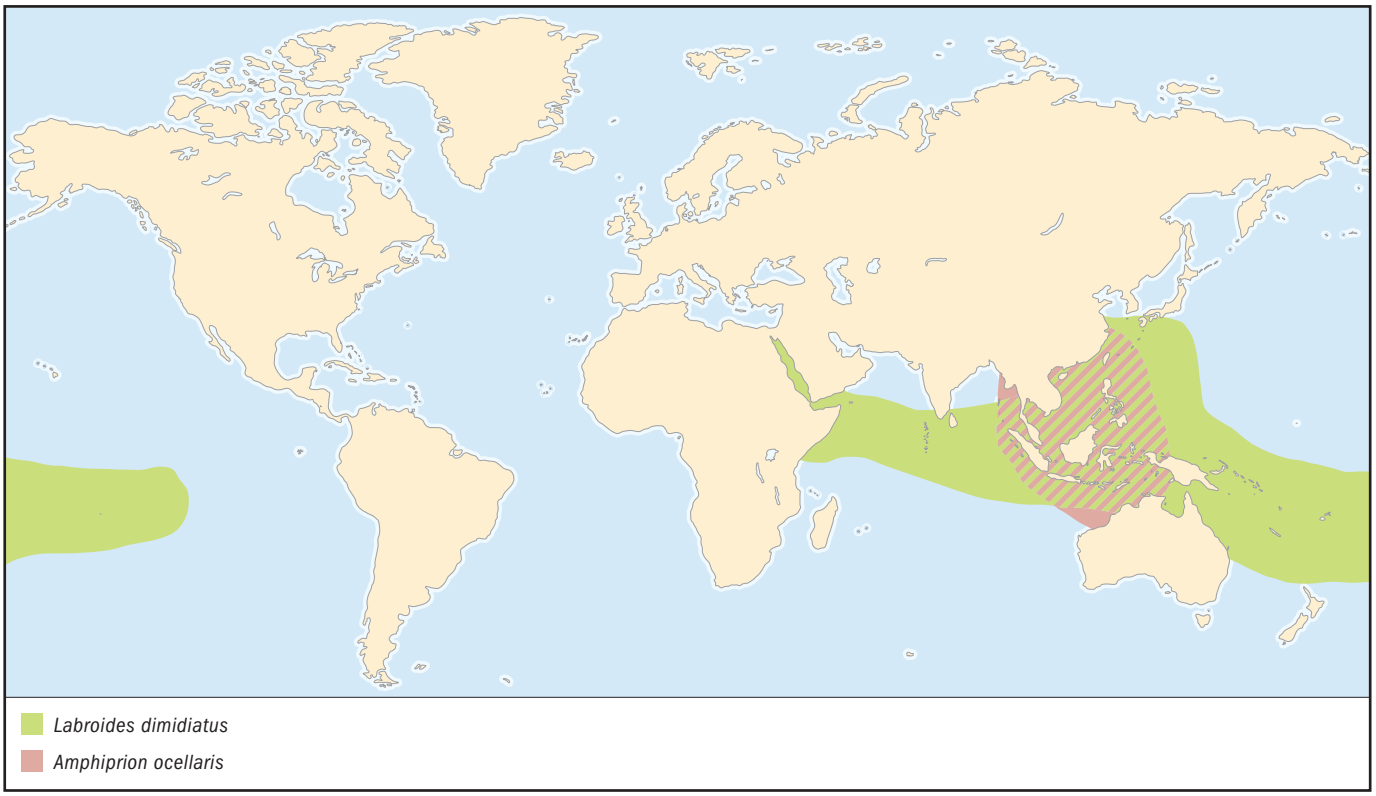
DISTRIBUTION
Throughout the Indo-Pacific region, west to the Red Sea and East Africa, north to the southern tip of Japan, and as far east as the Marquesas and Ducie Islands in the south central Pacific Ocean.

HABITAT
Prefers coral reef areas from surface waters to 130 ft (40 m) deep.

BEHAVIOR
Known for its cleaning habits, picking at and removing ectoparasites and assorted detritus on various species of fishes. Individuals or pairs set up stations, where they remove material from the bodies, gills, and even mouths of their "clients." Stereotyped signals between the two fishes help ensure that the cleaning goes smoothly, and the cleaner does not end up as the client's dinner.

FEEDING ECOLOGY AND DIET
Attains bulk of the diet from ectoparasites and detritus on other fishes.

REPRODUCTIVE BIOLOGY
Sometimes lives in pairs, but frequently in harems of one dominant male and 6–10 females. Sex reversal occurs when domi-



nant male is removed from a harem. The dominant female assumes his place, and becomes a functional male in about two weeks.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Common aquarium fish. ◆

Hogfish
Lachnolaimus maximus

FAMILY
Labridae

TAXONOMY
Lachnolaimus maximus Walbaum, 1792, type locality not specified (probably Bahamas or Carolinas).

OTHER COMMON NAMES
French: Labre capitaine; Spanish: Doncella de pluma.

PHYSICAL CHARACTERISTICS
Total length 36 in (91 cm). Often mottled, light orangey brown, but can adjust its color to match immediate surroundings. Adult dorsal fin sports three unusually long spines on anterior end. Dark stripe extends through eye to base of dorsal fin just behind head.

DISTRIBUTION
Bermuda, along the Atlantic coast of the Americas, from Nova Scotia to northern Venezuela, and into the southern and eastern Gulf of Mexico.

HABITAT
Sandy reef areas.

BEHAVIOR
Males are territorial, holding narrow areas about 100 yards (90 m) long. Around a dozen females share the territory with the male.

FEEDING ECOLOGY AND DIET
Prefers mollusks, crabs, and other hard-shelled invertebrates. Diurnal; during feeding ejects water streams into substrate to root out buried invertebrates.

REPRODUCTIVE BIOLOGY
Sex reversal is common. All fishes begin life as females, which can develop into males. No parental care is given to the pelagic eggs.

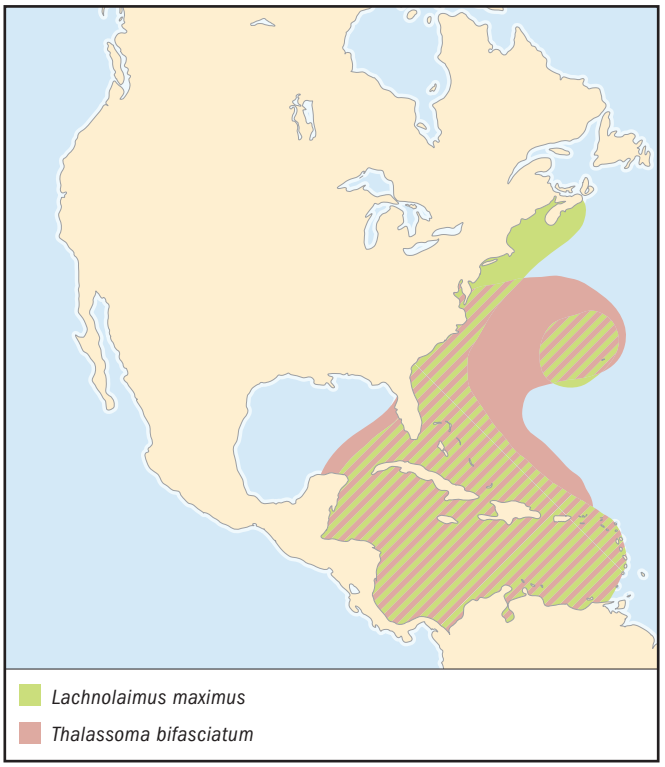
CONSERVATION STATUS
Listed as Vulnerable by the IUCN.

SIGNIFICANCE TO HUMANS
Commercial food fish. The large adult size and relatively sedentary character of this species make it particularly vulnerable to overharvesting.◆

California sheephead
Semicossyphus pulcher

FAMILY
Labridae

TAXONOMY
Semicossyphus pulcher Ayres, 1854, San Diego, California, United States.



OTHER COMMON NAMES
French: Labre californien; Spanish: Vieja de California.

PHYSICAL CHARACTERISTICS
Length 36 in (91 cm). Large teeth are a trademark. Initial-phase adults are orange with a white chin, terminal-phase adults retain orange coloration at midbody at white chins, but have black heads and rear bodies.

DISTRIBUTION
Subtropical waters in the Gulf of California, and off the west coast of North America, from Monterey Bay in central California, United States, south about 600 mi (966 km) to Guadalupe Island, Mexico.

HABITAT
Lives among kelp beds, in shallow, rocky-bottomed waters.

BEHAVIOR
Sex reversal is common, with females developing into males as they grow older.

FEEDING ECOLOGY AND DIET
Feeds on mollusks, crabs, sea urchins, and other invertebrates.

REPRODUCTIVE BIOLOGY
Protygynous, mating takes place each summer. No parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Commercial food fish. ◆

Bluehead
Thalassoma bifasciatum

FAMILY
Labridae

TAXONOMY
Thalassoma bifasciatum Bloch, 1791, East India (actually western Atlantic).

OTHER COMMON NAMES
English: Bluehead wrasse, tiki tiki; Spanish: Cara de cotorra.

PHYSICAL CHARACTERISTICS
Length 9.9 in (25 cm). Begins life as yellow, eventually develops black, horizontal stripes. Large terminal-phase males have vivid blue heads followed by white and black vertical bands, then green rear bodies and a bluish tail.

DISTRIBUTION
Western Atlantic Ocean near Bermuda, also from northern South America to the West Indies and southern Florida, United States, and into the Gulf of Mexico.

HABITAT
Coral reefs. Also seen among sea grass beds.

BEHAVIOR
Juveniles often provide cleaning services to other fishes. Among adults, spawning occurs differently depending on the size of the reef. On large reefs, group spawning is the rule. On small reefs, terminal-phase males utilize mating territories. Males from ensuing generations frequently use their ancestral mating site, apparently as a result of social convention. Dozens of females may select the same spawning site, and thus mate with the same male. Groups of smaller males often mate with egg-laden females by ambushing them on their way to the territorial mating sites.

FEEDING ECOLOGY AND DIET
Primarily feeds on drifting zooplankton, but also takes crabs, shrimps, sea urchins, and sea stars. Sometimes engage in cleaning of other species.

REPRODUCTIVE BIOLOGY
Engage in sex reversal. Over a period of several weeks, the black-striped, yellow males or females take on full coloration of large, terminal-phase males. Initial-phase females can take on the role of the terminal-phase male and begin producing sperm in as few as eight days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Aquarium fish. ◆

Butterfish
Odax pullus

FAMILY
Odacidae

TAXONOMY
Odax pullus Forster, 1801, Queen Charlotte Sound, New Zealand.

OTHER COMMON NAMES
English: Greenbone; Maori: Mararii.

PHYSICAL CHARACTERISTICS
Length up to 27.5 in (70 cm). Long dorsal fin begins just behind head, becoming increasingly wide as it draws to its posterior end. Males bluer than females, and have longer dorsal and anal fin tips.

DISTRIBUTION
Throughout New Zealand waters, with fisheries in the area of Cook Strait and Stewart Island.

HABITAT
Mostly occurs near the surface to 33 ft (10 m) deep, in waters heavy with kelp. Some live in sheltered areas, others prefer tidal zones.

BEHAVIOR
Diurnal, lives in small groups of one male and several females.

FEEDING ECOLOGY AND DIET
Adults move into more open reefs at dawn to begin grazing on red, green, and brown algae, particularly kelp, which they clip with beak-like mouths, then grind with pharyngeal jaws. Juveniles eat red algae and crustaceans.

REPRODUCTIVE BIOLOGY
Begins life as a female, and reverses sex as it matures. Mating occurs several times each year between females and territorial males, from late winter to early spring. A pelagic spawner.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sportfish and minor commercial food fish. ◆

Clown anemonefish
Amphiprion ocellaris

FAMILY
Pomacentridae

TAXONOMY
Amphiprion ocellaris Cuvier, 1830, Sumatra, Indonesia.

OTHER COMMON NAMES
English: Common clownfish, false clown anemonefish.

PHYSICAL CHARACTERISTICS
Total length 4.3 in (11 cm). Distinctive orange fish with three wide, vertical, white bands encircling the body just behind the eyes, at midback and in front of the tail. The fins and rounded tail are outlined in black, then edged in grayish white. Similar in general appearance to *A. percula.*

DISTRIBUTION
Coastal waters surrounding Indonesia; north and west to Burma, north and east past the Philippines to southern Japan, and as far south as northern Australia.

HABITAT
Prefers the sheltered shallow waters of lagoons, where it takes up residence among sea anemones.

BEHAVIOR
Most well known for its symbiotic relationship with the sea anemone. The clown anemonefish lives safely among the stinging cells, or nematocysts, of the anemone due at least in part to the specialized mucus layer that coats the fish. In this arrangement, the fish gains protection from predators, while the anemone receives a regular cleaning from the clown anemonefish. The fish has such a symbiotic relationship with four different species of sea anemones.

FEEDING ECOLOGY AND DIET
Eats mainly invertebrates that it often finds among the sea anemone's tentacles. Usually ventures only short distances from the shelter of the anemone, which has stinging tentacles. The sting deters most other species, making the anemone a safe haven.

REPRODUCTIVE BIOLOGY
Protandrous, lives in small groups in which all but two fishes are sexually immature males. The largest two in each group are sexually mature, with the larger being the only female in the group. If the female is removed, the sexually mature male develops into a sexually mature female, and the next largest has a growth spurt and becomes the sexually mature male. A dominance hierarchy controls the shift from male to female, and from immature to sexually mature.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Very popular marine aquarium fish. Many of the individuals sold are captive-bred. ◆

Blue chromis
Chromis cyanea

FAMILY
Pomacentridae

TAXONOMY
Chromis cyanea Poey, 1860, Cuba.

OTHER COMMON NAMES
Spanish: Cromis azul.

PHYSICAL CHARACTERISTICS
Total length 6 in (15 cm). Shimmering, blue with black dorsal shading, strongly forked tail, and dark eyes. Tail and belly also have some black coloration.

DISTRIBUTION
Western Atlantic Ocean near Bermuda, also from northern South America to the West Indies and into the Gulf of Mexico.

HABITAT
Reef fish, prefers deeper waters up to 200 ft (61 m) deep with coral overhangs and crevices where it can take shelter when threatened.

BEHAVIOR
Travels in sometimes multispecies schools, especially when feeding. Usually shy, will dash to the cover of reef when it feels threatened, and has been observed to dim its bright blue coloration to a duller gray.

FEEDING ECOLOGY AND DIET
Engages in group feeding of drifting zooplankton, but is territorial when feeding on algae and will defend an area against other algae-feeding species.

REPRODUCTIVE BIOLOGY
Male may spawn with several females and guards all eggs in his nest until hatching, which takes up to one week.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A popular commercial aquarium fish. ◆

Garibaldi damselfish
Hypsypops rubicundus

FAMILY
Pomacentridae

TAXONOMY
Hypsypops rubicundus Girard, 1854, Monterey, California, United States.

OTHER COMMON NAMES
English: Garibaldi; French: Chauffet Garibaldi; Spanish: Jaqueta vistosa.

PHYSICAL CHARACTERISTICS
Standard length 11.8 in (30 cm). Deep bodied, small mouthed, almost uniformly orange.

DISTRIBUTION
Occurs in subtropical waters off the west coast of North America from Monterey Bay in central California south about 600 mi (966 km) to Guadalupe Island, Mexico.

HABITAT
Lives in rocky-bottomed, reef-associated waters up to 100 ft (30.5 m) deep among and near caves, crevices, and other cover.

BEHAVIOR
Adults defend a home territory.

FEEDING ECOLOGY AND DIET
Feeds on vegetation and invertebrates, especially crustaceans, sponges, and worms.

REPRODUCTIVE BIOLOGY
Spawns in a bed of red algae, which the male prepares and tends. Courtship includes male visual and tactile displays. The female lays the eggs, the male guards them.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
State marine fish of California. ◆

Yellowtail damselfish
Microspathodon chrysurus

FAMILY
Pomacentridae

TAXONOMY
Microspathodon chrysurus Cuvier, 1830, St. Thomas Island.

OTHER COMMON NAMES
English: Jewelfish (as juveniles); French: Chaffet queue jaune; Spanish: Jaqueta rabo amarillo.

PHYSICAL CHARACTERISTICS
Length 8.3 in (21 cm). Juveniles typically dark blue with sky blue spots on all but the yellow tail. Adults are golden brown with dark-outlined scales and a yellow tail.

DISTRIBUTION
Western Atlantic Ocean near Bermuda, also from northern South America to the West Indies and southern Florida, United States, and into the southern Gulf of Mexico.

HABITAT
Shallow waters of shelter-filled coral reefs, usually associated with yellow stinging coral.

BEHAVIOR
When food is abundant, shares feeding area with other wrasses, but will weakly defend a territory if food is limited. Juveniles sometimes engage in cleaner activities.

FEEDING ECOLOGY AND DIET
Prefers grazing on algae, but also takes invertebrates, especially coral polyps.

REPRODUCTIVE BIOLOGY
Spawns mostly during semiannual periods. As males prepare nests, their coloration lightens. Female coloration brightens as they arrive to lay their eggs. Males tend and guard the eggs.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasional food fish and aquarium fish. ◆

Striped parrotfish
Scarus iseri

FAMILY
Scaridae

TAXONOMY
Scarus iseri Bloch, 1789, St. Croix Island, Virgin Islands, West Indies.

OTHER COMMON NAMES
English: Gray chub, mottlefin parrotfish; French: Perroquet rayé; Spanish: Jabón, loro rayado.

PHYSICAL CHARACTERISTICS
Total length 13.7 in (35 cm). Dark horizontal stripes are key feature of initial-phase individuals. Most prominent stripe is typically a center marking extending through the eye and nearly to the tail, where it narrows and fades. Juveniles are similarly patterned. Terminal-phase males are turquoise.

DISTRIBUTION
Lesser and Greater Antilles to southern Florida, United States, south along the South American coast to Brazil.

HABITAT
Prefers reef waters from the surface to 100 ft (30.5 m) deep.

BEHAVIOR
Typically schools, sometimes defends feeding territories if resources are limited or fish population numbers are high. Conspecific territorial displays include fanning of the ventral fins, opening of the mouth, and noncontact rushes toward one another.

FEEDING ECOLOGY AND DIET
Forms schools for feeding on algae, which it scrapes from rocks and other surfaces.

REPRODUCTIVE BIOLOGY
Initial-phase males and females may become terminal-phase males; female-to-male switch takes less than two weeks. Mating occurs year round, either in pairs or in groups. A broadcast spawner that gives no parental care to its pelagic eggs.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Minor commercial and aquarium fish. ◆

Stoplight parrotfish
Sparisoma viride

FAMILY
Scaridae

TAXONOMY
Sparisoma viride Bonnaterre, 1788, Bahamas.

OTHER COMMON NAMES
English: Moontail, parrot chub, redbelly; French: Perroquet feu; Spanish: Loro viejo.

PHYSICAL CHARACTERISTICS
Total length 25 in (64 cm). Females and younger adult males have mostly blue-gray body scales outlined in dark gray; reddish belly, tail, and fins. Colorful terminal-phase males mostly green, with blue and reddish horizontal stripes on head and lower ventral body, and yellow and blue markings on the tail, which is shaped like a crescent moon.

DISTRIBUTION
Western Atlantic from southern Florida, United States, to Brazil, also around Bermuda.

HABITAT
Juveniles prefer shallow sea grass beds and vegetated areas, adults inhabit coral reefs.

BEHAVIOR
Diurnal; lives alone or in small groups; moves to the sea bottom at night. Has been known to accept cleaning services from other species.

FEEDING ECOLOGY AND DIET
Feeds mainly on algae and other plants, but will eat corals. Feeding occurs only during the day. Will become territorial of feeding areas if food is limited.

REPRODUCTIVE BIOLOGY
Initial-phase individuals may be either male or female; terminal phase is male. Initial-phase females require three weeks to become terminal-phase males. Mating occurs year round.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Minor commercial and aquarium fish. ◆

Resources

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Michael, Scott W. *Reef Fishes: A Guide to Their Identification, Behavior and Captive Care.* Volumes 1–3. Shelburne, VT: Microcosm Ltd., 1998.

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Organizations

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Leslie Ann Mertz, PhD

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Zoarcoidei
(Eelpouts and relatives)

Class Actinopterygii
Order Perciformes
Suborder Zoarcoidei
Number of families 9

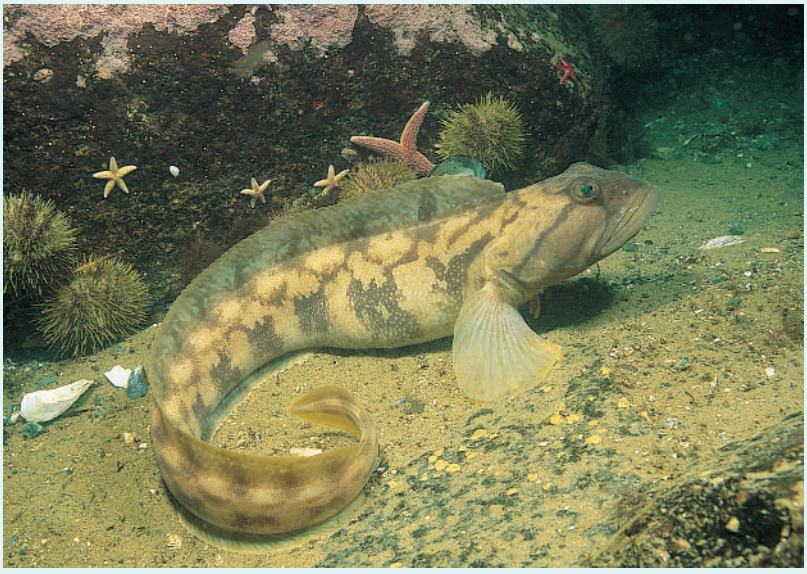


Photo: An ocean pout (*Zoarces americanus*) in the Gulf of Maine. (Photo by Andrew J. Martinez/ Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The zoarcoids, except for a few cryptic tidepool species, are a relatively obscure group of fishes of unverified affinity. On the basis of overall shape, fin structures, and position, and their ecological preference for living on sea bottoms in cold water, the most primitive family of zoarcoids, the ronquils, (Bathymasteridae) are thought to be close to the Antarctic "cods" or icefishes (suborder Notothenioidei). The zoarcoids and notothenioids share several important anatomical features, such as having only a single pair of nostrils, females with one ovary, lacking a gas bladder, and in having many similar skull characteristics. But they differ in other skull features and in the head sensory canal system slightly.

The time of appearance of the zoarcoids is unknown. Only the ear stones (otoliths) of an Upper Pliocene (3.2 to 1.9 million years ago) eelpout from southern California are known for the entire suborder's fossil record, and that species, *Lycodes pacificus*, is extant. If the zoarcoids are indeed related to the notothenioids, then we might construct an evolutionary scenario like this: In their 1966 classification of teleost fishes, Humphry Greenwood and colleagues noted that by the Eocene (57 to 35 million years ago), or possibly earlier (the view now taken by more evidence), marine inshore fish faunas had become composed of the groups that make up today's faunas. Sea floor spreading along tectonic plate boundaries separated Antarctica from Australia at the close of the Eocene, and for about the next 15 million years Antarctica drifted to its present position. As the Drake Passage deepened a circumpolar current, the Antarctic Polar Front, developed lying between latitudes 50° and 60° south, isolating Antarctica climatically. This spurred the creation of its ice cap and frigid sea temperatures. The notothenioids subsequently diversified rapidly here. This implies that prior to the Eocene, an ancestral group common to both zoarcoids and notothenioids split into two subgroups that developed physiological adaptations to the cold. One of these radiated throughout the Northern Hemisphere (zoarcoids) and the other across the cold Southern Hemisphere (notothenioids and the more primitive sandperches). Later re-invasions also took place, such as by deep-sea eelpouts (Zoarcidae) into the Southern Hemisphere and sandperches (Pinguipedidae) into the tropics.

As of 2002, science recognizes about 325 species of zoarcoids in about 100 genera and nine families, although further taxonomic work is needed and new species are discovered almost every year. Three families, the quillfish (Ptilichthyidae), the prowfish (Zaproridae), and the graveldiver (Scytalinidae) have only one species. Four of the familes are very small, with 6–7 ronquils (Bathymasteridae), five wolffishes (Anarhichadidae), four wrymouths (Cryptacanthodidae) and 14 gunnels (Pholidae). Thus only two families are sizeable, with 20% of all zoarcoids in the family Stichaeidae (pricklebacks) and 70% in the Zoarcidae (eelpouts).

An analysis of the relationships within Zoarcoidei has never been published. The ronquils were seen to be the most primitive family in having no advanced features common among the other families. The gunnels and graveldiver share a common, elongate shape and have lost the pleural ribs. Pricklebacks, gunnels, and the graveldiver have characteristic elongated crania not shared by the other families except for a few advanced eelpouts. However, many of the primitive pricklebacks, particularly the subfamily Stichaeinae, have many similarities to ronquils. The prowfish and wolffishes have similar shapes, large body size, fin structures, and features of the skeleton except for the skull and may be just generally primitive zoarcoids that split off the main lineage early in the group's

evolution at two different stages. Finally, the bizarre quillfish is so highly modified that its relationships are obscure. It is an extremely elongated fish (over 230 vertebrae) with many modifications of the head and fin structures and may represent another early offshoot of the main lineage that became highly modified rapidly, unlike the prowfish and wolffishes.

Physical characteristics

Two basic body shapes exist among zoarcoids. Primitively, a somewhat elongated, torpedo-like shape characterizes ronquils, some pricklebacks, wolffishes, and the prowfish; however, most pricklebacks and the wolffish *Anarrhichthys ocellatus* have attained a much elongated eel-like shape. All the eelpouts, gunnels, wrymouths, graveldiver, and the quillfish are eel-like in shape. Some eelpouts, especially the genus *Lycenchelys* and the quillfish are extremely elongated.

Most zoarcoids are small fishes reaching lengths of less than 15.8 in (40 cm). Some eelpouts attain 23.6 in (60 cm), and the largest of these, *Zoarces americanus*, reaches 46.5 in (118 cm). Other "giants" among the zoarcoids are the prowfish, reaching just over 3.3 ft (1 meter), and the wolffishes *Anarhichas* spp., reaching 47–57 in (120–145 cm), and *Anarrhichthys ocellatus*, the largest zoarcoid, which reaches 80 in (203 cm).

Deep-living, bottom-dwelling zoarcoids are rather somber in color, exhibiting more or less uniform shades of gray, brown, black, or purplish. Shallow-dwelling species can be more colorful, such as the prickleback genus *Chirolophis*, with shades of red, orange, and yellow, the ronquil genus *Rathbunella*, with its beautiful yellow and blue anal fin, and most of the gunnels, which show shades of green and brown to red reflecting the colors of the seaweeds among which they live. The dwarf wrymouth, *Cryptacanthodes aleutensis*, is uniformly red, and some North Pacific eelpouts, such as *Andriashevia aptera* and *Puzanovia rubra*, have also evolved this red to pinkish coloration. Sexual differences in coloration either do not exist or are usually subtle, with spawning males having dark anal fins, as in some gymneline eelpouts. However, the male prickleback, *Opisthocentrus ocellatus*, is normally drab grayish with dark markings but turns red with darker variegations in the spawning season.

Distribution

Ranges of the various zoarcoid groups can be confusing, especially in attempting to understand the pricklebacks and eelpouts; thus it is best to examine distributions on a family basis.

Bathymasteridae (ronquils): Central Sea of Japan, around the North Pacific rim to northern Baja California, Mexico.

Zoarcidae (eelpouts): In the Pacific from the northern Yellow Sea, east around the Pacific rim to the tip of South America and across the Scotia Arc to Antarctica. Four species are known from deep water in the tropical western Pacific. Distributed throughout the Arctic, especially the genera *Gymnelus* and *Lycodes* (*Lycodes frigidus* has been photographed in the Chukchi Sea at 78°28'N at a depth of 1.7 mi (2,653 m) and is probably widespread under the polar ice cap in suitable habitats). They live in the Atlantic from the Arctic south along the eastern United States to the Gulf of Mexico and Caribbean Sea; a few species are known from the Mid-Atlantic Ridge at hydrothermal vents. They also live in the eastern Atlantic from northern Europe, along the west African coast to South Africa. A few species of the deep-water genus *Pachycara* are known from the northern Indian Ocean abyss and may be widespread there. A few species of the mesopelagic genera *Lycodapus* and *Melanostigma* are circumpolar in subantarctic waters but do not reach coastal Antarctica, which has an endemic eelpout fauna.

Ptilichthyidae (quillfish): Hokkaido Island, Japan, around the North Pacific rim to central Oregon, United States.

Zaproridae (prowfish): Hokkaido Island, Japan, around the North Pacific rim to San Miguel Island, California.

Anarhichadidae (wolffishes): In the Pacific from Hokkaido, Japan, to the eastern Bering Sea (*Anarhichas lupus*) and the eastern Bering Sea to off southern California *(Anarrhichthys ocellatus)*. In the Atlantic (three species of *Anarhichas*) from Massachusetts to southern Greenland and east to the Kara Sea. The American wolffish, *Anarhichas lupus*, reached as far south as New Jersey in the nineteenth century.

Cryptacanthodidae (wrymouths): In the Pacific throughout the Sea of Japan north to Sakhalin Island, Russia *(Cryptacanthodes bergi)*; northern California to the Bering Sea (*C. aleutensis* and *C. giganteus*). In the Atlantic from New Jersey to Labrador (*C. maculatus*).

Stichaeidae (pricklebacks): In the Pacific from the northern Yellow Sea around the North Pacific rim to Baja California, Mexico. In the Atlantic from Massachusetts to Iceland, northern Norway, Britain, and throughout the Baltic Sea. A few species enter the Canadian Arctic; *Lumpenus medius* is circumpolar and even reaches the Sea of Japan.

Pholidae (gunnels): In the Pacific from the Yellow Sea around the North Pacific rim to Guadalupe Island, Baja California, Mexico. In the northwestern Atlantic from Delaware to Hudson Strait and the northeastern Atlantic from southern France to the Kara Sea including Iceland and Jan Mayen Island.

Scytalinidae (graveldiver): Central California (San Luis Obispo County) north to the Aleutian Islands, Alaska.

Habitat

The zoarcoids inhabit a wide variety of ecological niches and some have adapted to rather extreme habitats. At one end of this spectrum several gunnels, pricklebacks, and the graveldiver are found above the high tide line in rock pools with broad daily variation in temperature and salinity. Graveldivers also can be found burrowing in sand or gravel beaches above the surf wash. Most gunnels and pricklebacks are found in rocky areas with growths of seaweeds or invertebrate colonies, where they keep well hidden by day. In the opposite extreme many eelpouts are abyssal, or found on the bottom of the

A mosshead warbonnet (*Chirolophis nugator*) peering out from its hole. (Photo by Gregory Ochocki/Photo Researchers, Inc. Reproduced by permission.)

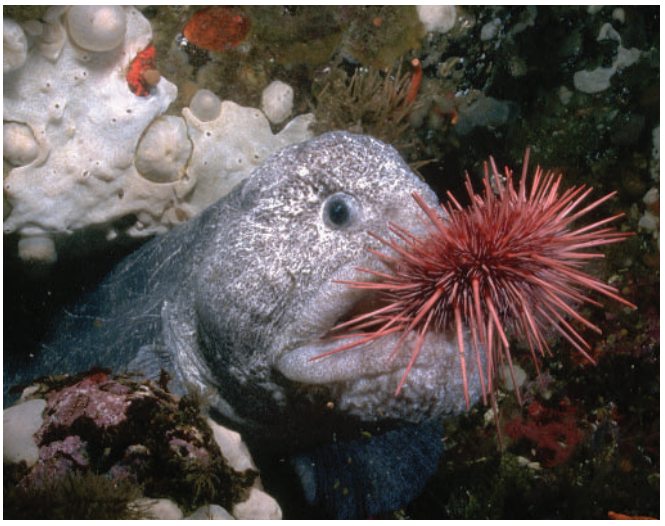
world's ocean basins, at depths of more than 4,375 yd (4,000 m). The deepest catch of a zoarcoid is that for a specimen of the eelpout *Lycenchelys antarctica*, trawled at 5,818 yd (5,320 m) in the Peru–Chile Trench by Russian researchers. Most eelpouts inhabit continental slopes of the North Pacific and North Atlantic, where bottom temperatures are below 44.6°F (7°C). Two eelpout genera, *Lycodapus* and *Melanostigma*, have adapted to a deep-water, free-swimming habit (in the mesopelagic zone), but have been photographed near the bottom. The ronquils are generally found in rocky reefs from inshore to about 301 yd (275 m). Nowhere very abundant, they are mostly seen by scuba divers in calm waters either in the rocks or over sandy patches. The wrymouths are mud burrowers and may be more active at night than in the day. The three Pacific wrymouths are found only in moderately deep water 33–383 yd (30–350 m), but the Atlantic species may be found in intertidal areas. The Atlantic wolffishes (genus *Anarhichas*) occur in rocky areas, never over muddy bottoms, generally on the outer shelf 109–328 yd (100–300 m), although the American species, *A. lupus*, has been seen in tidepools. The maximum depth is around 503 yd (460 m), although the three Atlantic species generally occur shallower to the north of their ranges. The Pacific wolffishes, *Anarhichas orientalis* and *Anarrhichthys ocellatus*, also occur in rocky reefs usually not deeper than 164 yd (150 m). All the wolffishes seem to lurk about in crevices and under overhangs when not foraging, sometimes in more open areas. The prowfish mostly occurs over soft bottoms of the outer shelf, but juveniles have been collected as shallow as 11 yd (10 m). One prowfish was caught in a trawl at 738 yd (675 m). Juvenile prowfish often occur in midwater where they may linger. The adult quillfish's habitat is probably free-swimming just above the bottom in outer shelf waters by day then migrating into surface waters at night to feed. One researcher speculated that it may burrow in mud, but without direct evidence.

Behavior

Most zoarcoids are cryptic and solitary throughout their lives, but may congregate in shelters or around food sources temporarily. Some deep-sea eelpouts have been photographed gathering around mammal carcasses and baited traps to feed on the amphipods that devour the carcass or bait. Some gunnels are known to share rock crevices for shelter. Social organization is not well documented in these hard-to-observe fishes. What behavioral patterns are known exist mostly as notes in the scientific literature from aquarium or scuba observations focusing mainly on reproduction. Nest guardianship has been noted for a few ronquils, pricklebacks, gunnels, eelpouts, and the wolf-eel, and this is discussed in the next section. During the winter in higher latitudes intertidal zoarcoids migrate into deeper water to avoid freezing, but populations are very localized and no great migrations occur. Thus, population movements are solely through larval dispersal by nearshore currents. Territoriality, as far as known, is probably weak among established adults of nearshore zoarcoids, since many share close spaces, but nothing is known of this in the deeper-living, cryptic species.

Feeding ecology and diet

The vast majority of zoarcoids are grazing predators of small invertebrates such as worms, crustaceans, molluscs, and echinoderms. Many switch prey items by season or as they age, but a significant number are dietary specialists, a situation often localized for a particular species. No in-depth study of the biology of the ronquils has been undertaken. Postlarvae (0.2–0.4 in [5–11 mm] in length) of *Ronquilus jordani* in southern British Columbia had been feeding near the surface on crustaceans (Cladocera, Copepoda, Cirrepedia larvae), clam larvae, and polychaete worms. The stripedfin ronquil, *Rathbunella hypoplecta*, is known to feed on the bottom primarily on crustaceans, but fish in one sample had fed exclusively on sea slugs (nudibranchs). A nest-guarding male *R. hypoplecta* had cannibalized part of his brood. Adult ronquils, then, are probably all opportunistic bottom grazers. The diets and feeding habits of a few eelpouts have been studied. Bottom-living species rely on crustaceans, particularly amphipods, but also eat smaller fishes, sea snails, clams, other kinds of crustaceans and, to a lesser extent, brittle stars and polychaete worms. The diets of the mesopelagic eelpouts *Lycodapus mandibularis* and *Melanostigma pammelas* off California diversify with increasing size but mainly consist of a few kinds of crustaceans. Young pricklebacks of several species in the water column off British Columbia feed on copepods and clam larvae. As they grow and settle into bottom habitats, a dietary shift occurs and most adult pricklebacks then rely on polychaetes, amphipods, sea snails, nudibranchs, various kinds of algae, bryozoans, shrimps, crabs, and sponges. Although this appears to be a rather diverse diet when several species are examined from different areas, many of the xiphisterine pricklebacks are herbivores, eating only a few kinds of red and green algae. Atlantic pricklebacks have been recorded with similar diets: amphipods, copepods, ostracods, brittle stars, clams, sea cucumbers (Holothuria) and polychaetes. Gunnels, living among rocks and seaweeds with pricklebacks, feed on the same prey. The Atlantic butterfish, *Pholis gunnellus*, eats various mollusks,



A large male wolf-eel (*Anarrhichthys ocellatus*) eats a sea urchin. (Photo by Brandon D. Cole/Corbis. Reproduced by permission.)

especially sea snails, crustaceans, and polychaetes, and has been known to raid other fishes' nests to consume their eggs. In the Canadian Pacific, *Pholis ornata* and *Pholis laeta* are known to switch diets with age. Both mostly rely on harpacticoid copepods when young, but large fish shift mostly to caprellid amphipods (*P. laeta*) or clam siphons (*P. ornata*). Young wrymouths in the Canadian Pacific also rely on copepods when feeding in midwater. The diets of adults are not well recorded, but food recorded for the Atlantic wrymouth consists of various crustaceans, mollusks, and fish. The wolffishes all have canine teeth in the front of their jaws and viselike molars in the back, dental adaptations for dealing with hard-shelled prey. The Atlantic wolffishes prey on mollusks like whelks, cockles, clams, and mussels as well as large crabs, hermit crabs, starfish, and sea urchins, the latter rather formidable as food. The Pacific wolf-eel, *Anarrhichthys ocellatus*, eats mostly commercial crabs (*Cancer magister*) and other hard-shelled invertebrates. Fish rarely enter the diets of wolffishes. Not much is known of the food habits of the prowfish, graveldiver, or quillfish. Young prowfish are free-swimming and are known to associate with jellyfish. Remnants of amphipods that also associate with jellyfish, as well as jelly fragments, have been found in stomachs of large prowfish. Thus they may utilize various jellyfishes as a food source, at least in part, throughout their life. Graveldivers are burrowers and probably hunt tiny interstitial invertebrates. The quillfish, with its small, upturned mouth and free-swimming habits, probably preys on a variety of small planktonic crustaceans and mollusc larvae.

Reproductive biology

Because nearshore zoarcoids are generally small, cryptic fishes and offshore species usually live beyond scuba depths, almost all observations on the reproductive biology of these fishes come from aquarium observations on a few nearshore species. A few zoarcoids captured from scientific research vessels have been examined in some detail, but generally little about their reproduction is known.

Direct observations on courtship are few, and fertilization is internal in all known bottom-living species. Males of the elongate zoarcoids (eelpouts, gunnels, pricklebacks, wolf-eel) wrap around receptive females snake-like and fertilization is internal, or eggs are fertilized as they are laid in clusters. The pectoral fins in courting male viviparous eelpouts (*Zoarces viviparus*) turn bright red and males assume a characteristic coiled position with the fins outstretched. When females are receptive males then assume a transverse position under and alongside the female for mating. Pelagic eelpouts like *Lycodapus* may have little formal courtship behavior and probably just pair up during a protracted spawning season and release eggs and milt into the water column. The northern ronquil (*Ronquilus jordani*) has a rather long courtship with the male displaying to the female with body and fin quivering and fanning. It is generally assumed that most of the nearshore zoarcoids spawn during daylight hours when they can see one another for courting, but the Japanese tidepool gunnel (*Pholis nebulosa*) courts and spawns from about midnight to dawn.

Egg size and number vary greatly in zoarcoids, owing to the variation in adult body size. Reported sizes range from about 0.1–0.3 in (1–7 mm), but the eggs of the quillfish, graveldiver, and prowfish are unknown. Fecundity ranges from less than 20 eggs per female in some primitive eelpouts (Gymnelinae) to about 50,000 in one wolffish. Eggs can be clear, white, yellowish, or orange with oil droplets usually yellow, orange, or red, and most are adhesive since they are laid in nests. Incubation times range from about two weeks to three months. Yolk sac larvae of bottom-living zoarcoids generally stay near the bottom, but some become planktonic for anywhere from a few seconds to minutes (*Zoarces americanus*), or up to two years (*Anarrhichthys ocellatus*).

Nests are generally simple hideaways among most zoarcoids. Ronquils lay loose egg masses on flat surfaces, which are fanned and usually guarded by the male. In the stripedfin ronquil (*Rathbunella hypoplecta*), there is an aquarium observation of a female laying eggs six times every two weeks for a total of about 10,000 eggs during the three months. A new clutch was laid just days after the most recent spawn hatched, and the male guarded the egg mass. Bottom-living eelpouts excavate a crater in muddy bottoms and coil around a clump of eggs. However, the Atlantic midwater eelpout (*Melanostigma atlanticum*) is known to burrow tunnels into soft muddy bottoms with a male and female spawning, but sometimes several apparently non-spawning individuals may occupy the tunnels to help circulate water in this anoxic environment. Gunnels and pricklebacks lay eggs on seaweeds (*Zostera*, some algae) or in nests in rock crevices and holes; some gunnels are known to use empty oyster or mussel shells. Wolffishes build nests in rocky shelters or lay their eggs among seaweeds and stones.

Parental care is fairly limited in most zoarcoids that are known for this behavior. The male of the smooth ronquil noted above sometimes ate some of the eggs he was guarding. Guardianship of nests may be limited to fanning with charging displays against intruders (ronquils) or of parents holing up with the eggs with no overt signs of care simply because the nest area provides good cover (gunnels and pricklebacks).

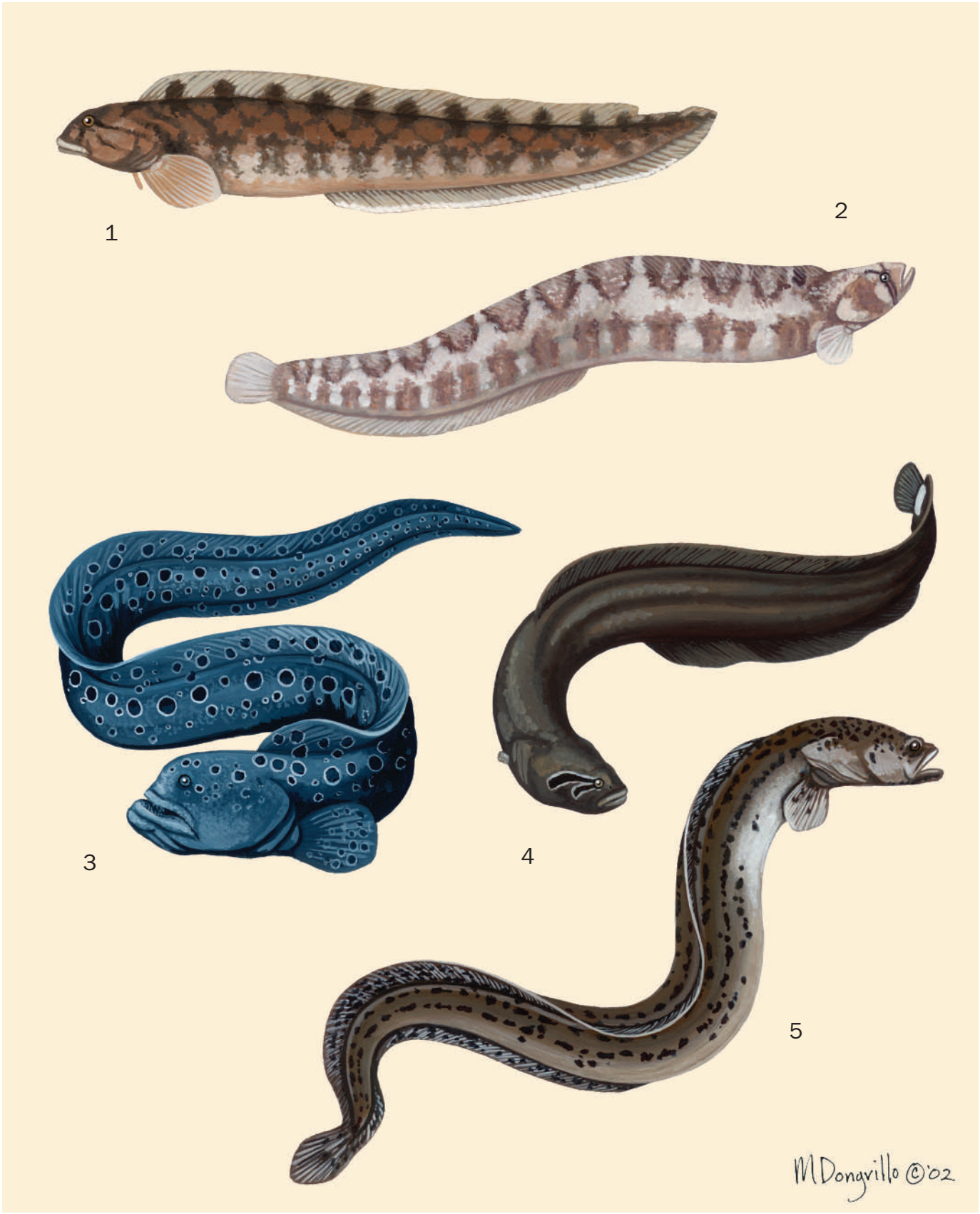
The spawning season of zoarcoids can be short, just a few months between courtship and egg hatching, or protracted into the better part of a year. Some deep-sea eelpouts spawn only once or twice at the end of their lives, and seasonality may not exist for these. Ronquils and many gunnels and pricklebacks spawn from the spring to summer; other gunnels and pricklebacks are autumn to winter spawners. The North Atlantic wolffishes spawn from spring to winter, and the more northerly populations start earlier in the year than southern populations. The northwestern Atlantic wrymouth (*Cryptacanthodes maculatus*) is a winter spawner, but the Japanese wrymouth (*Cryptacanthodes bergi*) spawns from spring to summer. On the basis of larval captures in scientific collecting nets, quillfish spawn at least in spring but probably have a longer season. Nothing is known of the spawning habits of the prowfish or graveldiver.

Conservation status

Most nearshore zoarcoids are fairly common in their preferred habitats. This includes most ronquils, gunnels, pricklebacks, shallow-dwelling eelpouts, and wolffishes where they're not fished. Other species are rare, and this is a result of either naturally low population densities or that they are rarely caught or seen, such as the graveldiver, prowfish, and quillfish. No zoarcoids have been considered endangered or threatened, mostly owing to these fishes' usually cryptic habits and limited commercial use.

Significance to humans

The zoarcoids are a fairly insignificant group of fishes in human history. No mythology or significant art or literature exists, but it is interesting to note that in the Middle Ages it was commonly held that the European viviparous eelpout (*Zoarces viviparus*) was said to birth all eels (order Anguilliformes), owing to its live-bearing mode of reproduction. Significant fisheries do not exist for any zoarcoid today. However, after World War II a minor longline fishery for wolffishes (*Anarhichas*) developed across the North Atlantic, but catches have declined dramatically since. An unsuccessful attempt was made to develop a fishery for the American ocean pout (*Zoarces americanus*) after World War II, but natural parasitic infections in the flesh quickly killed the plan. No zoarcoid poses any real danger to humans except wolffishes. Trawl-caught *Anarhichas* species have been known to snap at fishermen and a large, speared wolf-eel (*Anarrhichthys ocellatus*), because of its strength and imposing teeth, may inflict serious bites to careless scuba divers.



1. Ocean pout (*Zoarces americanus*); 2. Saddleback gunnel (*Pholis ornata*); 3. Wolf-eel (*Anarrhichthys ocellatus*); 4. Black prickleback (*Xiphister atropurpureus*); 5. Wrymouth (*Cryptacanthodes maculatus*). (Illustration by Marguette Dongvillo)

Species accounts

Wolf-eel
Anarrhichthys ocellatus

FAMILY
Anarhichadidae

TAXONOMY
Anarrhichthys ocellatus Ayres, 1855, San Francisco, California.

OTHER COMMON NAMES
English: Pacific wolfeel.

PHYSICAL CHARACTERISTICS
Body eel-like. Dorsal and anal fins long and low, continuous with a small caudal fin. Pectoral fins large and fan-like. Pelvic fins absent. Background color blue, greenish, brown, or gray-brown. The body and head are covered with white-lined black spots. Scales are small and rounded and embedded in the skin. There is no lateral line canal. The teeth in front are canine-like, and the rear teeth are molar-like. Juveniles are orangish brown, with spots more numerous and larger than in adults; the spots sometimes form into stripes. This is the largest zoarcoid, reaching 2.2 yd (203 cm).

DISTRIBUTION
Southeastern Bering Sea to off Imperial Beach, California. Records for the Sea of Japan or Kamchatka are erroneous.

HABITAT
Deep rocky reefs in caves or crevices. Juveniles are free-swimming for an extended period.

BEHAVIOR
Cryptic and solitary or lives with an apparent life-long mate in a den. It is a dusk and dawn predator but also feeds during the day. Territorial disputes occur with large individuals displacing mated pairs occasionally.

FEEDING ECOLOGY AND DIET
Stalking predator. Feeds mainly on hard-shelled invertebrates and occasionally fish. Wolf-eels grab their prey with their enlarged canines and crush it with their rear molars. Known prey consists of crabs, clams, mussels, sea urchins, sand dollars, snails, and abalone. A population of wolf eels at the head of the Monterey submarine canyon in California has relied on sand dollars at least seasonally, a food presumably rather low in nutrition for its bulk. Free-swimming juveniles eat plankton and small fish.

REPRODUCTIVE BIOLOGY
Pairs form at about four years of age (length about 3.3 ft [1 m]), and eggs are first laid at about seven years. Spawning occurs from October to February. Courtship consists of the male repeatedly bumping the female's abdomen; when she is receptive he coils around her snake-like. Eggs are fertilized as they are laid in clumps of about 7,000–10,000, and the female gathers these up into a ball and wraps around them, occasionally turning them for aeration. Both parents guard the nest, and only one at a time leaves to forage. Hatching occurs at 13–16 weeks, depending on water temperature. Juveniles are free-swimming for up to two years, then settle on open bottom until they take up their sedentary den life.

CONSERVATION STATUS
Not threatened. This species is common and widespread along its range. A minor fishery exists among scuba divers, skiff fishermen, and bottom trawlers.

SIGNIFICANCE TO HUMANS
The wolf-eel is a good eating fish, and the scuba and small boat fishery has been significant and sustained in some areas of central California and Puget Sound, Washington. Wolf-eel teeth have been found in a native American village site in central California, indicating a fishery at least 9,000 years old. Tribes in the Pacific Northwest reserved this delicacy for their shamans. ◆

Wrymouth
Cryptacanthodes maculatus

FAMILY
Cryptacanthodidae

TAXONOMY
Cryptacanthodes maculates Storer, 1839, off Massachusetts, United States.

OTHER COMMON NAMES
English: Congo eel, ghostfish; French: Terrassier tacheté.

PHYSICAL CHARACTERISTICS
Body eel-like. Head flattened above. Eyes small. Mouth large and up-turned. Pectoral fins small. Pelvic fins absent.

Dorsal and anal fins long, low, and continuous with caudal, which is well developed. Background color brown to reddish brown, with 2–3 irregular rows of dark brown spots or blotches running from head to tail. The dorsal and anal fins have rows of smaller brown spots. Abdomen pale gray. Scales absent.

DISTRIBUTION
Southern Labrador south to New Jersey.

HABITAT
Found from just above the low tide mark (the intertidal zone) to almost 656 yd (600 m). Constructs branching tunnels in riverine mudflats, where it lives singly. May live in burrows or hide in crevices or under rocks in deeper water.

BEHAVIOR
Due to their secretive burrowing habits, there have been no observations on natural behavior. One wrymouth was kept in an aquarium, where it could not burrow. It lived instead in a piece of rubber tubing. Thus it is likely that they hide almost all the time and venture forth only to forage.

FEEDING ECOLOGY AND DIET
Grazing or ambush predator. Feeds on small crustaceans (amphipods, shrimps, and hermit crabs), mollusks (limpets, sea snails, clams, and mussels), and occasionally fishes.

REPRODUCTIVE BIOLOGY
Eggs and larvae are unknown, but wrymouths undoubtedly spawn on the bottom and probably guard nests. Fry have been collected in scientific sampling nets in early spring, indicating winter spawning.

CONSERVATION STATUS
Rarely seen. Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Saddleback gunnel
Pholis ornata

FAMILY
Pholidae

TAXONOMY
Gunnellus ornatus Girard, 1854, San Francisco, California.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body eel-like. Pectoral fin small and half as long as the head. Pelvic fins are minute, mere splints. Dorsal and anal fins continuous with a caudal, which is well developed. Color can change from olive-green to brown dorsally; abdomen yellow to reddish. There is a dark bar under the eye and two above the eye across the head. There are several (about 13–15) U-shaped or V-shaped markings ("saddles") along the base of the dorsal fin reaching onto it. No lateral line canal. Scales minute, rounded, and embedded in the skin.

DISTRIBUTION
Northern Vancouver Island, British Columbia south to Carmel, California.

HABITAT
Migrates seasonally from brackish, estuarine mudflats and subtidal sea grass beds under rocks in autumn to deeper water out to about 44 yd (40 m), where its major competitor, *Pholis laeta*, occurs. Where that species does not co-occur with the saddleback, some remain in the intertidal zone year-round. The young settle in the rocky intertidal or shallow channels in winter and move into more brackish water later.

BEHAVIOR
Solitary and cryptic. Aggregates for spawning. Probably not territorial.

FEEDING ECOLOGY AND DIET
Grazer. Dietary shifts correlated with age. In British Columbia the young feed mainly on small crustaceans (copepods) and polychaete worms, while older fish switch to clam siphons, relying less on small crustaceans (copepods and tanaids).

REPRODUCTIVE BIOLOGY
Spawns in rocky intertidal or deeper sea grass beds under rocks in winter. There is probably a single spawning of one male and one female; both parents guard the eggs. Larvae are pelagic for a brief period and settle in rocky intertidal areas then move into brackish mudflats with seasonal growth of seaweeds, at least in bays and estuaries.

CONSERVATION STATUS
Not threatened. Common and widespread along its range. It is cryptic and rarely encountered by humans.

SIGNIFICANCE TO HUMANS
Because of its secretive habits and small size, there has never been a fishery for the saddleback gunnel, and it does not make a good aquarium fish. Thus the species has been of little significance to humans. ◆

Black prickleback
Xiphister atropurpureus

FAMILY
Stichaeidae

TAXONOMY
Ophidium atropurpureum Kittlitz, 1858, Alaska (no specifics). Correct generic placement should probably be in *Xiphidion* Girard, 1858 (or 1859), pending further research.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body eel-like. Pectoral fins are minute, of only 11 or 12 rays. Pelvic fins absent. Dorsal and anal fins continuous with caudal, which is well developed and has a whitish band at its base. Color reddish brown to black; abdomen is lighter. Head has three broad, black eye bars with whitish borders. Scales are minute, rounded, and covered with skin.

DISTRIBUTION
Kodiak Island, Alaska south to Baja California Norte, Mexico.

HABITAT
Intertidal zone in rock pools among seaweeds and in crevices out to about 32.8 ft (10 m). Also found under wharf pilings and in boat harbors where shelter (human trash usually) can be found.

BEHAVIOR
Solitary and cryptic without territoriality. Parental care of the eggs occurs (see below).

FEEDING ECOLOGY AND DIET
Omnivore. Feeds on seaweeds and invertebrates on or associated with the bottom, primarily crustaceans, worms, and sea snails. Hatchlings caught in surface-towed nets in British Columbia had been feeding on copepod crustaceans and clam larvae but probably eat any small planktonic animals.

REPRODUCTIVE BIOLOGY
Spawning occurs from winter to spring throughout the range, under rocks along protected pebbly or shelly beaches in winter and shifting to other beaches that are more exposed in spring. Females lay about 900–1,700 eggs about 0.1 in (2 mm) in diameter, and males guard the site. Males may spawn with more than one female. Territoriality is non-existent in that several males may congregate under the same rock, and sometimes other species, such as clingfishes, are found nearby. Hatchlings are about 0.3 in (8.5 mm) long, and metamorphosis occurs at about 0.7 in (18 mm) when they become free-swimming and feed on small plankton.

CONSERVATION STATUS
Not threatened. Common and widespread along its extensive range. It is cryptic and rarely encountered by either humans or predators.

SIGNIFICANCE TO HUMANS
Owing to its secretive habits and small size there has never been a fishery for the black prickleback, and it does not make a good aquarium fish; thus the species has been of little significance to humans. ◆

Ocean pout
Zoarces americanus

FAMILY
Zoarcidae

TAXONOMY
Blennius americanus Bloch and Schneider, 1801, American seas.

OTHER COMMON NAMES
English: Muttonfish, yowler; French: Loquette d'Amérique.

PHYSICAL CHARACTERISTICS
Body eel-like but rather stout in adults. Pectoral fins large and fan-like. Pelvic fins have short splints. The dorsal and anal fins are continuous with the caudal fin; the dorsal fin has about 15–25 tiny spines at its rear. Background color usually muddy yellowish, tinged with brown above and becoming darker with age. Belly usually yellowish but can be olive-green. Mottling on the sides is brown, but the pattern is individually variable. Teeth are green in northern populations owing to predation on sea urchins. Scales are minute, round, and not overlapping.

DISTRIBUTION
Southern Labrador south to Virginia.

HABITAT
Adults found on the outer shelf to about 219 yd (200 m) on sandy or muddy bottoms. Young may come into intertidal areas among seaweed and rocks. Free-swimming hatchlings sometimes found in estuaries of large rivers to the north.

BEHAVIOR
Very little is known of behavioral traits in ocean pout, mostly owing to the difficulty of observing them in their usual offshore habitat. Based on aquarium observations, they probably live passive, solitary lives without territories and seem only to

congregate for spawning. Spawning consists of several copulations over many hours. Large spawning males are aggressive to smaller males at this time, as are females with non-spawning females. Parental care of the eggs occurs (see below).

FEEDING ECOLOGY AND DIET

Grazer. Feeds on invertebrates on or within the sea floor, mostly on crustaceans (amphipods, *Cancer* crabs, and hermit crabs especially), sea urchins, worms, bivalves (clams and scallops), sea snails, and brittle stars. Fish found in a few stomachs occasionally are probably scavenged.

REPRODUCTIVE BIOLOGY

Spawning occurs in early to mid-Autumn and consists of males approaching ripe females and rolling on their sides or even upside down under the female. Fertilization is internal and several copulations occur for 2–3 minutes each over many hours, perhaps up to half a day. Egg laying occurs around 6–17 hours after the last copulation. Large females lay a clutch of eggs in rocky areas more numerous than smaller females. A female at nearly 35.4 in (90 cm), near the maximum size, contained over 4,100 ripe eggs; another at 21.6 in (55 cm), and probably spawning for the first or second time, had 1,300 eggs. The eggs are pale yellow and measure 0.24–0.28 in (6–7 mm) in diameter. Upon laying her egg mass the female fans and wipes her skin over the eggs for around 30 minutes. This coats the mass in an antibiotic mucus. Then the female wraps herself tightly around the mass (now white in color), which helps stick it together into an egg ball. Females remain passive while guarding their eggs except for intermittent swimming in circles while fanning the eggs with their pectoral fins. Incubation lasts for three months, during which females probably do not feed much. Fry hatch in mid-winter, and yolk sac resorption occurs in seconds. Fry have a very short planktonic phase while working their way inshore, where they develop over the first few years of their lives.

CONSERVATION STATUS

Not threatened. Common in nearshore environments as young where predation is probably low. Also common offshore even on the fishing banks off New England and Nova Scotia.

SIGNIFICANCE TO HUMANS

A minor fishery for ocean pout began in Massachusetts in the 1930s, with fish being sold "round" in Boston markets. In 1943, as a war effort, a concerted attempt was made to sell whole fillets, and landings reached almost 4.4 million lb (2 million kg) in 1944. However, ocean pout are afflicted with a microsporidian (Protozoa) parasite that produces unsightly lesions in the flesh. Landings dropped to under 6,100 lb (2,767 kg) by 1948, and the fishery subsequently failed. Attempts to revive the fishery in the 1970s also failed. ◆

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Notothenioidei
(Southern cod-icefishes)

Class Actinopterygii
Order Perciformes
Suborder Notothenioidei
Number of families 8

Photo: A scuba diver observes a blackfin icefish (*Chaenocephalus aceratus*) as it swims off the coast of Signy Island, one of the South Orkney Islands near the Antarctic Peninsula. (Photo by Rick Price/Corbis. Reproduced by permission.)

Evolution and systematics

Over the past 40 million years, the suborder Notothenioidei has evolved in high latitudes of the Southern Hemisphere from generalized blennioid ancestors, producing a remarkable variety of ecological, morphological, physiological, and biochemical specializations. This diversity has led to their recognition as the only known example of a marine species swarm, rivaling the freshwater swarms of cichlid fishes in the African rift lakes and the landlocked cottoids of Lake Baikal. Over the past three decades, intensive study of the group has been driven by the increase in internationally funded research in Antarctica that followed the Antarctic Treaty of 1959.

The basic taxonomic framework for the suborder, established in the early 1900s, recognized five families; as of 2002, the Notothenioidei included 122 species in 43 genera, divided into eight families:

- Bovichtidae (thornfishes, 10 species in two genera); the most primitive family
- Pseudaphritidae (one catadromous species, *Pseudaphritis urvillii*, the Australian congolli or tupong)
- Eleginopidae (one species, *Eleginops maclovinus*)
- Harpagiferidae (spiny plunderfishes, six species in one genus)
- Artedidraconidae (plunderfishes, 25 species in four genera)
- Nototheniidae (notothens, or "Antarctic cods," 49 species in 12 genera)
- Bathydraconidae (dragonfishes; 15 species in 11 genera)
- Channichthyidae (icefishes, 15 species in 11 genera)

There are no unequivocal notothenioid fossils; thus, little is known of the origins of the suborder. Earlier claims of Eocene and Miocene notothenioid fossils from the Antarctic Peninsula and New Zealand have been discounted. The only substantial Antarctic fish fossils are found in Eocene deposits on Seymour Island, near the Antarctic Peninsula. These beds contain a cosmopolitan shallow-water fossil fish fauna that is completely different from the modern Antarctic fauna, presently dominated by notothenioids. As Antarctica became glaciated, the hardy notothenioids replaced the earlier fishes and then diversified under the impetus of habitat destruction associated with cyclical glacial advances.

Physical characteristics

Notothenioids have a diversity of sizes and body forms. Most are small fishes, on the order of 1 ft (30 cm) in length, but some species may be as small as 4.3 in (11 cm) or as long as 6 ft (1.8 m). None is highly colored; most have black, brown, or gray mottling on paler backgrounds. They have two to three lateral lines on the trunk and well-developed sensory canals on the head, jaw, and pre-operculum. Three plate-like radials characterize the pectoral girdle. All notothenioids lack a swim bladder.

Many of the 96 species of Antarctic notothenioids coexist with sea ice, near the freezing point of seawater (28.6°F, or −1.87°C). They are protected from freezing by an antifreeze

glycopeptide (AFGP), consisting of repeating groups of three amino acids (-alanine-alanine-threonine-)$_n$, with a disaccharide (galactose-N-acetylgalactosamine) attached to each threonine. AFGP works differently from normal colligative antifreezes such as salt or glycol, which only depend on the number of ions or molecules to lower freezing temperature. Instead, AFGP molecules bind to mircroscopic ice crystals and interfere with the attachement of additional water molecules, preventing ice from growing to a size that would damage living cells. Thus a very small number of AFPG molecules can have a disproportionate effect on freezing. The gene encoding AFGP has evolved from part of a gene for the digestive enzyme trypsin.

As well as being important for survival, AFGPs are metabolically expensive. In the high-latitude notothenioids that produce AFGPs, changes in the kidney reduce their loss. Instead of forming urine by pressure filtration in capillary bundles (glomeruli), Antarctic notothenioids eliminate wastes by selective secretion into the urine, and AFGPs are retained. Their kidneys lack the glomeruli characteristic of most other vertebrates. In contrast, the 26 species of notothenioids living outside Antarctic waters rarely encounter freezing seawater, lack AFGPs, and have glomeruli.

Distribution

Three of the eight notothenioid families are primarily non-Antarctic:

- Bovichtidae: These are found mainly north of the Antarctic convergence, in Australia/Tasmania, southern New Zealand, and southern South America. One species occurs along the Antarctic Peninsula.
- Pseudaphritidae: The family inhabits streams and estuaries of southeastern Australia and Tasmania.
- Eleginopidae: These fishes are confined to southern South America.

The remaining five families have distributions that are primarily Antarctic or subantarctic:

- Harpagiferidae: The family is found mainly in sub-Antarctic regions, from Patagonia, the Falkland Islands, South Georgia, and the Scotia Arc to the tip of the Antarctic Peninsula and in Kerguelen, Crozet, and Heard Islands.
- Artedidraconidae: These fishes are exclusively Antarctic, from South Georgia along the Scotia Arc to the Antarctic Peninsula and around continental Antarctica.
- Nototheniidae: Thirty-four species are truly Antarctic, and the remainder occur in sub-Antarctica, Patagonia, and southern New Zealand.
- Bathydraconidae: The family occurs in the Antarctic, from South Georgia along the Scotia Arc and around the Antarctic continent.
- Channichthyidae: The family is confined primarily to the Antarctic but has one species in Patagonia/Falkland Islands. The other 14 species are found from South Georgia through the Scotia Arc and around the Antarctic continent; they also occur in the Bouvet and Kerguelen Islands but not as far as the Heard, Campbell, or Auckland Islands.

Habitat

Notothenioids are widespread in coastal waters of the Southern Ocean, on or over the continental shelf. Their depth range is from the surface to 1,370 fathoms (2,500 m). Aside from their dispersive larval stages, most avoid the open ocean, living on or near the bottom as adults. Several species of Nototheniidae and Channichthyidae have abandoned their ancestral benthic existence, however, to move up into the water column, becoming pelagic. Lacking swim bladders, these midwater forms have increased buoyancy in other ways. Their bones are less mineralized than those of demersal species, and they have high oil contents. One widespread pelagic species, the sardine-like nototheniid *Pleuragramma antarcticum*, retains larval features, including a persistent notochord surrounded by greatly reduced vertebral centra.

Behavior

Notothenioids tend to be sedentary bottom species that swim infrequently. Where swimming has been observed, it is labriform, propelled by undulatory sculling of the pectoral fins. The trunk and tail are used only for short, fast dashes. Even the pelagic forms are relatively inactive.

Feeding ecology and diet

Demersal notothenioids are generalized predators. Some forage nonselectively; others are ambush predators. Pelagic species, such as *P. antarcticum*, are more selective, feeding on copepods, larger midwater crustacea (e.g., krill, such as *Euphausia superba*), and pteropods (e.g., *Limacina*). In turn, these smaller midwater fishes are eaten, along with krill and squid, by the few large mesopelagic fish (such as the toothfish, *Dissostichus mawsoni*), by birds (penguins, skuas, and petrels), and seals. *D. mawsoni* is eaten by Weddell seals (*Leptonychotes weddelli*) and by killer whales (*Orcinus orca*).

Reproductive biology

Many Antarctic and subantarctic notothenioids breed biennially, with oocytes taking two years to ripen. Eggs are large and yolky and usually are spawned on or near the bottom. Spawning times differ with latitude and between species, ranging from early spring to early winter. Embryonic development and growth are slow, and most larvae hatch 6–12 months after spawning. The larval stages are pelagic, settling to the bottom after feeding in the plankton for six to nine months.

Conservation status

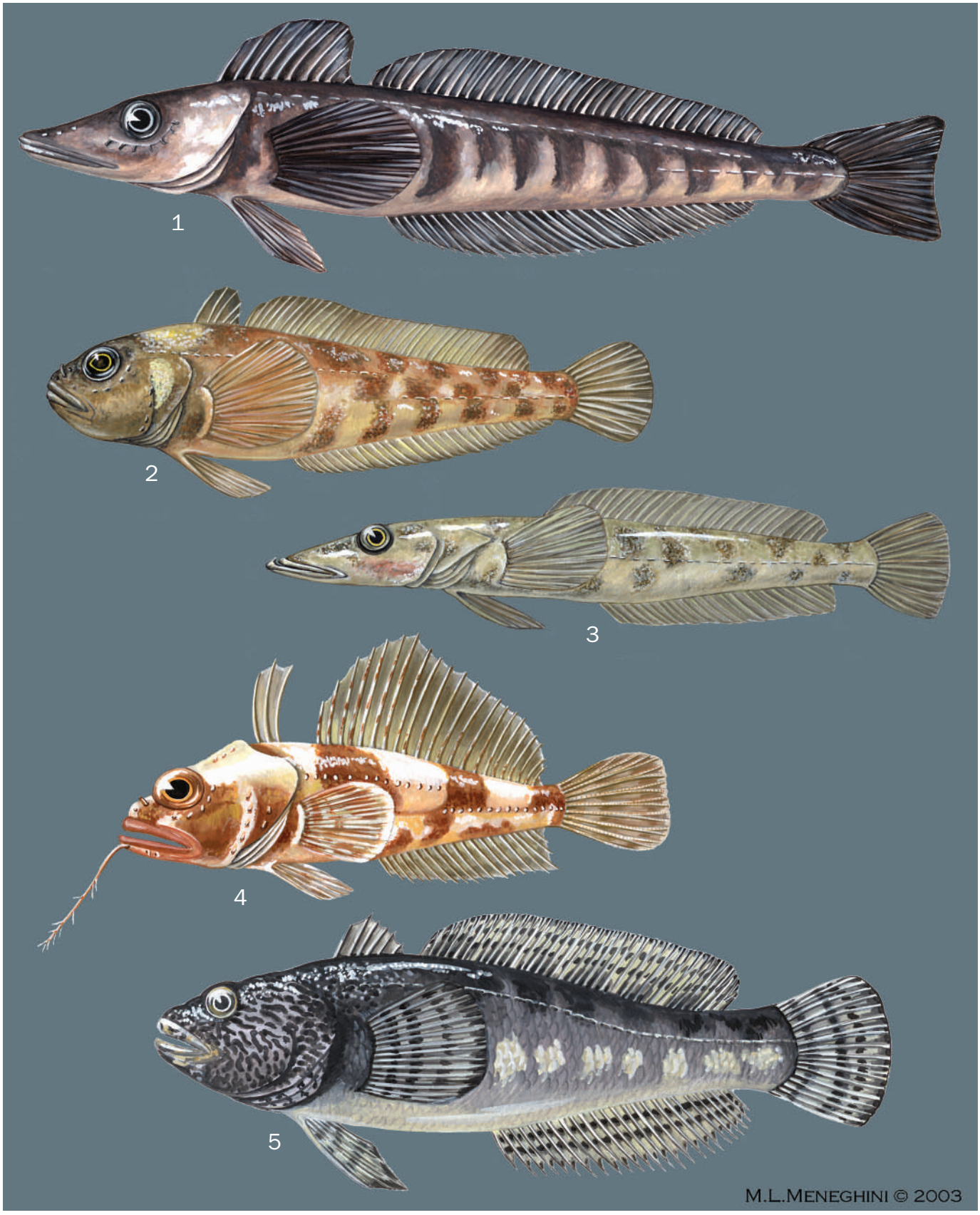
None of the notothenoids are on the IUCN Red List. Although the majority of notothenioids are not exploited and have

widespread and abundant populations, several species have been the target of fisheries. The marbled rockcod, *Notothenia rossii*, has been seriously overfished but is no longer targeted, and it is recovering, albeit slowly. The Patagonian toothfish, *Dissostichus eleginoides*, has been exploited since the 1980s and has been given the designation of data deficient in a report on the conservation status of Australian fishes complied by the Threatened Fishes Committee of the Australian Society for Fish Biology.

After depleting the South Georgia/Falkland Islands toothfish fishery, attention shifted to Macquarie and Kerguelen Islands and then further west, to the southern Indian Ocean. In the mid-1990s the estimated illegal catch exceeded the legal catch, but in 1999 the Commission for the Conservation of Antarctic Marine Resources implemented a strict catch-reporting regime for toothfish, reducing the 1999/2000 illegal catch to an estimated 8,418 tons (7,637 tonnes), of a total 33,660 tons (30,536 tonnes). Since 1996 there has been a limited exploratory fishery for the closely related Antarctic toothfish, *D. mawsoni*, in the Ross Sea, where a catch of 1,000 tons (907 tonnes) was reported in 2001. Because most notothenioids share characteristics of low fecundity and slow growth, their fisheries are highly susceptible to overfishing and should be monitored closely.

Significance to humans

Some notothenioids have been harvested for fish meal and oil (e.g., *P. antarcticum*), but the group is exploited mainly for human consumption. The mackerel icefish, *Champsocephalus gunnari*, is the basis of small, but sustainable fisheries near South Georgia and the Kerguelen Islands. There is a ready market for the two toothfish species, *D. eleginoides* and *D. mawsoni*, which are highly palatable.



1. Mackerel icefish (*Champsocephalus gunnari*); 2. Emerald notothen (*Trematomus bernacchii*); 3. Naked dragonfish (*Gymnodraco acuticeps*); 4. Sailfin plunderfish (*Histiodraco velifer*); 5. Maori chief (*Notothenia angustata*). (Illustration by Michelle Meneghini)

Species accounts

Sailfin plunderfish
Histiodraco velifer

FAMILY
Artedidraconidae

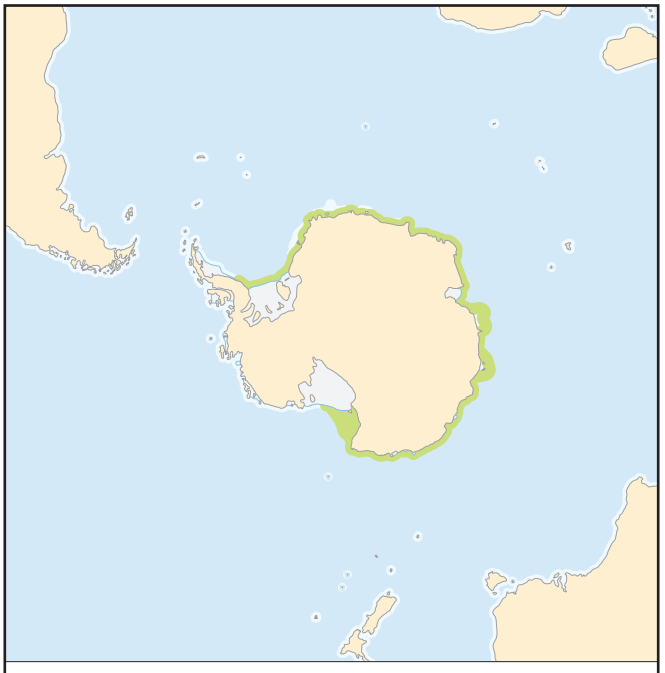
TAXONOMY
Dolloidraco velifer Regan, 1914, McMurdo Sound, Antarctica.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Attains a length of up to 7.5 in (19.2 cm) (length/depth ratio, 5:1). It has a large, depressed head with a conspicuous barbel on the chin; this barbel is one of the characteristic features of the family. The first dorsal fin is tall and narrow, consisting of only three flexible spines, and is directly above the operculum. The second dorsal fin is disproportionately tall and sail-like. The second dorsal, caudal, pectoral, and pelvic fins have brown and yellow striations. The body color is a light tan, with irregular dark blotches. Scales are absent, except for parts of the two lateral lines on the trunk.

DISTRIBUTION
Coastal waters of Antarctica, from the Weddell Sea clockwise to the Ross Sea.

HABITAT
This is a bottom-dwelling fish, found at depths of 48–2,190 ft (15–667 m). It is taken occasionally by scuba divers on the mud or gravel bottoms in McMurdo Sound and Terra Nova Bay.



BEHAVIOR
In the aquarium, the sailfin plunderfish sits quietly on the bottom. The barbel is extended and occasionally twitched, mimicking a small worm. Histological examination shows that the barbel is highly innervated, with many tiny capsules resembling Pacinian corpuscles (a comomn type of pressure-sensitive sense organ amongst the vertebrates). Touching the barbel with forceps elicits a feeding lunge. This behavior implies that natural feeding may target mobile foragers, such as fish and amphipods.

FEEDING ECOLOGY AND DIET
Very little is known about the diet of the sailfin plunderfish, other than what can be inferred from behavioral observations in the aquarium. Where they have been examined, gut contents include krill and polychaete worms. Like most of the benthic notothenioids, it is probably an opportunistic feeder.

REPRODUCTIVE BIOLOGY
Nothing is known of the reproductive biology, as very few specimens have been collected.

CONSERVATION STATUS
Although this is an uncommon species, poorly represented in museum collections, it is not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Naked dragonfish
Gymnodraco acuticeps

FAMILY
Bathydraconidae

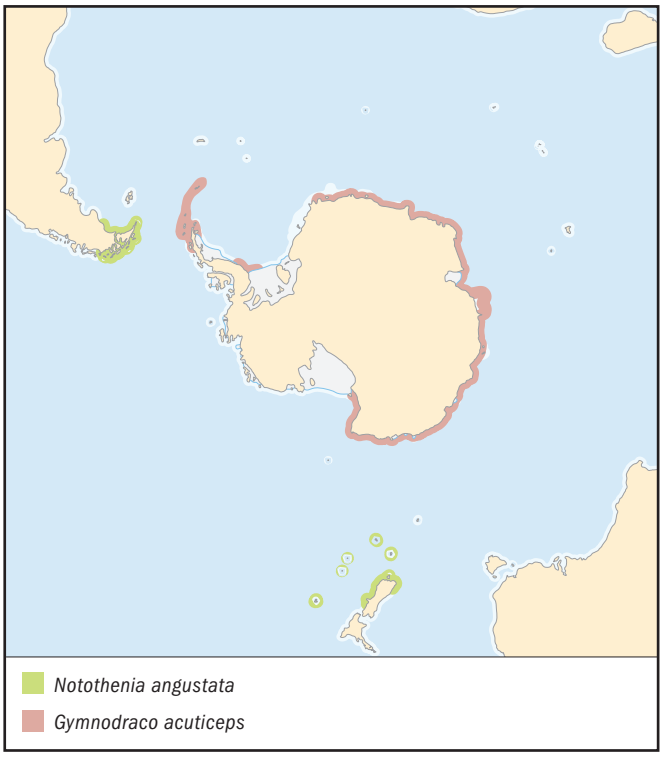
TAXONOMY
Gymnodraco acuticeps Boulenger, 1902, Cape Adare, North Victoria Land, Antarctica.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Grows to 13.5 in (34 cm) in length. It has an elongated, scaleless body (length/depth ratio, 9:0) with a long, pointed head. The coloring is yellowish to olive-brown, with darker blotches on the sides; it is pale on the ventral surface. The lower jaw extends well beyond the upper and bears two prominent fangs that are slanted backwards to prevent the escape of prey. In common with all members of the dragonfish family, it lacks the first spinous dorsal fin. This species produces abundant mucus when it is freshly caught.

DISTRIBUTION
South Shetland, the Antarctic Peninsula, and the eastern Antarctic continental shelf from the Weddell Sea to the Ross Sea.

HABITAT
Found mainly in shallow inshore waters, to a depth of 162 ft (50 m), although it has been caught as deep as 1,800 ft (550 m). It commonly resides in crevices or under rock ledges or anchor ice.



BEHAVIOR
This is an aggressive fish that rapidly consumes other aquarium inhabitants.

FEEDING ECOLOGY AND DIET
The diet varies with location. Near the Antarctic Peninsula, the dragon fish feeds on krill; in McMurdo Sound, fish, amphipods, fish eggs, and polychaetes are taken.

REPRODUCTIVE BIOLOGY
Spawning occurs in September; 0.12-in (3-mm) eggs are attached to a stone as a flattened patch of about a thousand and guarded. In the wild, adults tend egg masses until the larvae hatch and disperse. Development takes about a year. Free-swimming larvae, about 0.6 in (15 mm) long, hatch out in early summer and remain in the zooplankton for about six months.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
This species is proving to be a valuable research subject. Beginning in 2001 clusters of developing embryos near McMurdo Station have been harvested for investigation into the ontogeny of AFGPs. ◆

Mackerel icefish
Champsocephalus gunnari

FAMILY
Channichthyidae

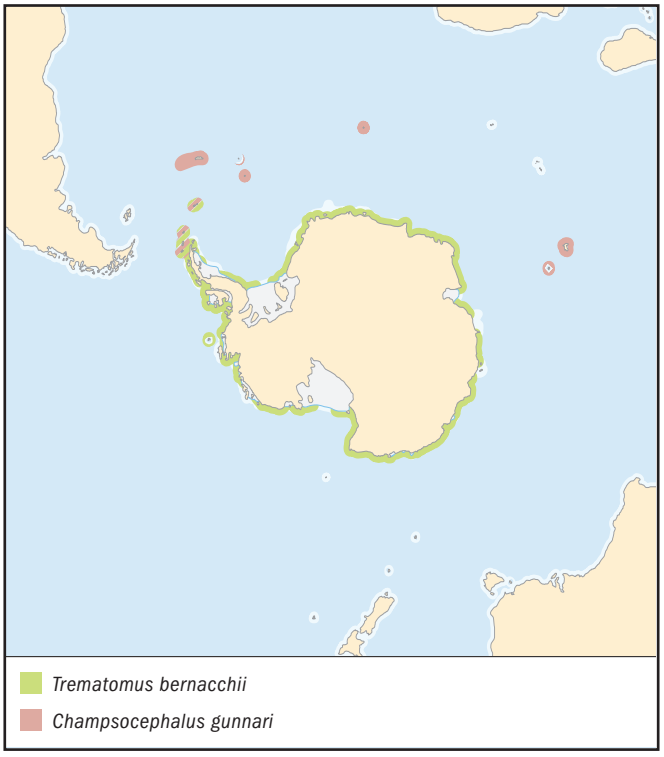
TAXONOMY
Champsocephalus gunnari Lönnberg, 1905, Cumberland Bay, South Georgia.

OTHER COMMON NAMES
English: Crocodile icefish, pike glassfish; French: Poisson des glaces; Spanish: Draco rayado; Russian: Ledyanaya ryba.

PHYSICAL CHARACTERISTICS
Elongated, scaleless, pikelike body (length/depth ratio, about 7:2) with an elongated snout. The jaws do not protract. In coloring it is silvery gray, darker on the back, and silvery on the belly, with dark vertical stipes on the sides, reminiscent of those seen in mackerel. The gills are a pale yellowish; the blood is colorless, completely lacking hemoglobin. The absence of hemoglobin is a remarkable feature of all 15 icefish species, apparently caused by a single massive mutation that deleted the β-globin gene. Far from being an adaptation to Antarctic conditions, this has been termed a "disaptation." Several factors have enabled channichthyids to survive this evolutionary catastrophe: frigid seawater and blood plasma can carry more dissolved oxygen, and low body temperatures limit metabolic requirements. Subsequent evolution has compensated for the loss of an oxygen-binding pigment: blood volume, heart, vessel, and gill size and the perfusion rate of gills and blood vessels all have increased. As a consequence, channichthyids are surprisingly active, competing successfully with other notothenioids.

DISTRIBUTION
South Georgia and the islands of the Scotia Arc, southward to the northern Antarctic Peninsula; it also inhabits Bouvet, Kerguelen, and Heard Islands. A closely related species, *C. esox*, occurs in the Falklands Islands and Patagonia and is the only channichthyid to occur outside Antarctic/subantarctic waters.

HABITAT
This is a coastal species, found mainly between 330 and 1,140 ft (100–350 m). Mature adults are found offshore in summer, moving inshore to spawn in the fall (March–May).



BEHAVIOR
The species aggregates in locations with dense krill populations, remaining near the bottom during the day and migrating upward with the krill at night.

FEEDING ECOLOGY AND DIET
The mackerel icefish feeds mainly on krill (*Euphausia superba*); it takes other euphausiids, mysids, and hyperiid amphipods (*Themisto gaudichaudii*) when krill numbers are low.

REPRODUCTIVE BIOLOGY
Reproductive parameters vary considerably between the different stocks. Maturation of oocytes takes less than a year, producing 1,300–31,000 eggs that are 0.12–0.16 in (3–4 mm) in diameter. When krill are scarce, oocytes may be resorbed, and as many as 60% of mature females may be nonreproductive. A marked three-year periodicity in reproduction is reported from the Kerguelen stock. Near South Georgia, spawning occurs from March to May; it takes place later in South Orkney and South Shetland and as late as July to August in the Kerguelen stock. Eggs are deposited in the depth range of 330–660 ft (100–200 m) and hatch after 30–180 days, depending on the stock. Newly hatched larvae are 0.05–0.07 in (12–17 mm) long and feed on copepods within 12 mi (20 km) offshore; larger juvenile fish move further offshore but remain over the continental shelf. Juveniles grow at 2.5–3.5 in (6.4–8.9 cm) per year, reaching sexual maturity at three years at a length of 10 in (25 cm).

CONSERVATION STATUS
Not listed by the IUCN. The various stocks of mackerel icefish have been targeted by minor trawl fisheries since 1974. Catches fluctuate from year to year, but they appear to be sustainable for the South Georgia and Kerguelen stocks. In South Orkney and South Shetland, the stock was depleted rapidly below sustainable levels and is no longer being fished.

SIGNIFICANCE TO HUMANS
A total catch of 4,295 tons (3,896 tonnes) was reported from the Commission for the Conservation of Antarctic Marine Resources management area in 1999–2000. ◆

Maori chief
Notothenia [Parenotothenia] angustata

FAMILY
Notothenidae

TAXONOMY
Notothenia angustata Hutton, 1875, Dunedin Harbour, New Zealand.

OTHER COMMON NAMES
English: Black cod.

PHYSICAL CHARACTERISTICS
Grows to 2 ft (60 cm) in length. Mature specimens have a massive body (length/depth ratio, 5:1) with a large, slightly flattened head; heavy bony ridges over the eyes; and large scales. The coloring is dark olive-gray to blue-black, with varying light spots and lines; there are vague dark vertical bands on the trunk. Juveniles are less flattened, with deeper bodies, deard reddish bronze coloring, and prominent light spots.

DISTRIBUTION
Southern waters of New Zealand, from Stewart Island to Kaikoura. It also is found in Chatham, Snares, Auckland, and Campbell Islands and in Punta Arenas, Chile, and adjacent water.

HABITAT
Adults are demersal on rocky bottoms, from near shore to 330 ft (100 m) depth. Juveniles are found in tide pools and among kelp near the shore.

BEHAVIOR
Like most other notothenioids, the Maori chief is solitary and never occurs in schools. Adults are shy and sedentary, foraging among rocks and seaweed mainly at night. During the day, they hide in crevices or under seaweed, occasionally lunging for passing prey. Smaller fish are sucked into their mouth by the sudden expansion of the jaws and opercula. Juveniles are more active than adults, often leaving the bottom to forage in the upper layers of kelp beds.

FEEDING ECOLOGY AND DIET
The Maori chief feeds on a wide range of bottom invertebrates, crabs, and smaller fishes. Occasionally, it ingests seaweed.

REPRODUCTIVE BIOLOGY
The life cycle of the Maori chief is not well known. Eggs ripen in November and presumably are deposited on the bottom. Juveniles appear in rock pools in the summer (January) after an incubation period of about 30 days and a brief pelagic dispersal phase.

CONSERVATION STATUS
Not listed by the IUCN. This species was caught for the local market up to the 1950s, when stocks were reported to be overfished. There is currently no commercial fishery for this species, nor has it been assigned a quota under New Zealand's quota management system.

SIGNIFICANCE TO HUMANS
This is said to be a palatable species, but its fearsome appearance and coarse texture relegate its use mainly to bait in lobster pots. ◆

Emerald notothen
Trematomus bernacchii

FAMILY
Nototheniidae

TAXONOMY
Trematomus bernacchii Boulenger, 1902, Cape Adare and Duke of York Island, North Victoria Land, Antarctica.

OTHER COMMON NAMES
English: Emerald rockcod, bernak; French: Bocasson émeraude; Russian: Trematom-pestryak; Spanish: Austrobacalao esmerelda.

PHYSICAL CHARACTERISTICS
Reaches a maximum length of 12 in (30 cm) and a maximum weight of 12.3 oz (350 g). It is thick-bodied (length/depth ratio, about 3:9) and light brown to pinkish brown on the sides, with irregular darker blotches; the belly is silvery gray. It is covered with ctenoid scales, except for a patch between the eyes, where there may be a single row of scales. Three distinct color varieties are known:

- continuous white band across the nape and opercula
- an interrupted band, consisting of a narrow medial stripe on the nape and on each operculum
- no white marking

DISTRIBUTION
Coastal waters of Antarctica, including the Antarctic Peninsula and South Shetland and South Orkney Islands.

HABITAT
It is most common on boulder, rock, or gravel bottoms or in sponge beds at depths of 18–1,200 ft (5–370 m), but it has been caught as deep as 2,280 ft (700 m). Smaller individuals are found in shallow water, whereas mature fish are more common in deeper water.

BEHAVIOR
The emerald notothen is a sedentary demersal species, spending most of its time immobile on the bottom. It swims infrequently and slowly, sculling with the pectoral fins and making short excursions across the bottom or ascending about 3 ft (1 m) into the water column. In the aquarium, dominant individuals establish and defend territories.

FEEDING ECOLOGY AND DIET
This is an opportunistic feeder and scavenger, primarily on benthic invertebrates. Small crustaceans are the most common dietary item, followed by polychaetes, molluscs, fish, and fish eggs. It ingests seaweed, but its nutritional contribution is unknown.

REPRODUCTIVE BIOLOGY
The life span of the emerald notothen is 8–10 years; in McMurdo Sound, first spawning occurs at five years. Females spawn biennially; initial oocyte development takes one year and active vitellogenesis (deposition of yolk within the growing egg) another year. Spawning takes place over a brief period, from October to November in Adélie Land and December to January in McMurdo Sound. Fecundity is on the order of 1,500–3,000 eggs, which are attached to rocks, algae, or sponges; mature eggs are 0.16 in (4 mm) in diameter. There are reports that the emerald notothen tends egg masses in sponges.

CONSERVATION STATUS
Not threatened. The emerald notothen is widespread and common; considering its small size and high latitude, it is not likely to come under any significant pressure from fisheries. Its limited mobility probably would lead to extremely rapid depletion of any local populations that might be subjected to commercial fishing.

SIGNIFICANCE TO HUMANS
This species has played an important scientific role in the study of anatomical, physiological, and biochemical adaptations to the Antarctic environment. Most significantly, it has featured prominently in the elucidation of biological antifreeze compounds. ◆

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Resources

Organizations

Australian Society for Fish Biology. 123 Brown Street (PO Box 137), Heidelberg, Victoria 3084 Australia. Phone: 61 (3) 9450 8669. Fax: 61 (3) 9450 8730. E-mail: john.koehn@nre.vic.gov.au Web site: <http://www.asfb.org.au>

Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). PO Box 213, North Hobart, Tasmania 7002 Australia. Phone: 61 (3) 6231 0366. Fax: 61 (3) 6234 9965. E-mail: ccamlr@ccamlr.org Web site: <http:/www.ccamlr.org>

TRAFFIC International. 219c Huntington Road, Cambridge, CB3 0DL United Kingdom. Phone: 44 (0) 1223 277427. Fax: 44 (0) 1223 277237. E-mail: traffic@trafficint.org Web site: <http://www.traffic.org>

Other

Prof J. T. Eastman, Ohio University. "Antarctic Fishes." (March 27, 2003) <http://www.oucom.ohiou.edu/dbms-eastman/index.htm>

John A. Macdonald, PhD

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Trachinoidei

(Weeverfishes and relatives)

Class Actinopterygii
Order Perciformes
Suborder Trachinoidei
Number of families 13

Photo: A four-spined sandperch (*Parapercis tetracantha*) in the Balayan Bay of Luzon Island in the Philippines. (Photo by Fred McMonnaughey/Photo Researchers. Reproduced by permission.)

Evolution and systematics

A group of fishes referred to as the "trachinoids" was recognized in 1860 and has undergone significant modification over the years, with several groups variously added or subtracted and then added again. The current notion of the Trachinoidei actually is quite similar to that of 150 years ago, although a few groups have been put in the group that were not described at that time. The Trachinoidei is almost certainly an unnatural grouping of fishes, meaning that there is little evidence to suggest that its included families are related more closely to each other than they might be to any perciform family outside the trachinoids. Pietsch, and then Pietsch and Zabetian, offered the first comprehensive modern phylogenetic studies of relationships within the suborder. They did not include Pholidichthyidae and Trichodontidae in their surveys, considering the examined taxa to represent "the core of, but not necessarily to delimit," the suborder. Their results, listed sequentially in phylogenetic order (with each group being the sister to all remaining taxa) were as follows: i) Cheimarrichthyidae; ii) Pinguipedidae; iii) Percophidae, Trichonotidae, and Creediidae; iv) Champsodontidae and Chiasmodontidae; v) Leptoscopidae; vi) Ammodytidae; vii) Trachinidae; and viii) Uranoscopidae.

Johnson, and later Mooi and Johnson, reexamined much of the data and determined that many of the features used to define trachinoid relationships by Pietsch and Zabetian are distributed widely among many perciforms and do not necessarily indicate close affinity. The families themselves seem to be natural groups, except the Percophidae. In this grouping, the members of the percophid subfamily Hemerocoetinae exhibit derived features of the suspensorium, indicating a phylogenetic relationship with the Creediidae and Trichonotidae to the exclusion of the percophid subfamilies Percophinae and Bembropinae. Mooi and Johnson refuted any close relationship between Champsodontidae and Chiasmodontidae, suggesting that the former more likely has relatives among the Scorpaeniformes and that relatives of the remaining trachinoid families might be searched for more fruitfully among other perciforms rather than among themselves. Mooi and Johnson hinted that trichodontids might be scorpaeniforms, but Nazarkin and Voskoboinikova suggested a new suborder for the family, emphasizing its differences from other trachinoids but not resolving its enigmatic phylogenetic position. McDowall maintained that the monotypic Cheimarrichthyidae should be considered a member of the Pinguipedidae. The relationships of the Pholidichthyidae also are unclear.

The fossil record of trachinoids is scant. A member of the Trachinidae is described from the base of the Middle Eocene from Monte Bolca, Italy (about 49 million years ago, or mya). Reported from the Agnev Formation (Upper Miocene, about 10 mya) of Sakhalin Island, Russia, are a species of Trichodontidae and a species put in a new family, the Trispinacidae, which is considered to be related to the Pinguipedidae.

There are 13 families with 235+ species in 53 genera: Ammodytidae (seven genera, 27 species), Champsodontidae (one genus, 13 species), Cheimarrichthyidae (monotypic), Chiasmodontidae (four genera, 15+ species), Creediidae (seven genera, 16+ species), Leptoscopidae (three genera, five species), Percophidae (11 genera, 44 species), Pholidichthyidae (one genus, two species), Pinguipedidae (five genera, 50 species), Trachinidae (two genera, four species), Trichodontidae (two genera, two species), Trichonotidae (one genus, six species), and Uranoscopidae (eight genera, 50 species).

Physical characteristics

Not surprisingly, given that most families are not related closely, physical characteristics vary considerably among trachinoids. Ammodytids, the sand lances, are small to moderate sized, growing to about 16 in (40 cm). They have narrow, elongate bodies with small heads. The lower jaw protrudes beyond the upper, and there are no teeth in the jaws. These fishes have a single long dorsal fin without spines and reduced or absent pelvic fins. The body has a series of oblique folds of skin called plicae. Ammodytids swim with a distinctive eel-like undulation that makes them easy to identify in the water. Champsodontids, the gapers, are small, growing only to 6 in (15 cm), but they are large-headed, with a large mouth armed with long teeth. There is a large spine on the preopercle and two dorsal fins, the first with four to six spines. The pectoral fin is very small, but the pelvic fin is quite large. The body is covered with spinoid, nonoverlapping scales that are raised above the body surface by a small pedicle; a series of sensory papillae can be found between the scales.

Cheimarrichthyids, the New Zealand torrentfishes, are smaller than 8 in (20 cm), with a broad, somewhat flattened, wedge-shaped head; subterminal mouth; a robust, scaled body with a long, soft dorsal fin preceded by three to five short spines; and large pectoral and pelvic fins. Chiasmodontids, the deep-sea swallowers, are moderately sized bathypelagic fishes, growing to 10 in (26 cm). They are elongate, with a large head, a large mouth with enormous teeth, a rugose head pitted with sensory pores, a scaleless body that sometimes has prickles, a large-pored lateral line, and two separate dorsal fins, the first with seven to 13 flexible spines. These fishes have a hugely distensible gut that permits them to eat prey twice their own size, giving rise to their common name. Some species bear photophores. Creediids, the sandburrowers, are the smallest trachinoids, at 1.5–3.0 in (3.5–8 cm). They are elongate, with slightly protruding eyes, a fleshy snout projecting beyond the lower jaw, and a scaled body with a single dorsal fin and reduced pelvic fins. Leptoscopids, the southern sandfishes, reach about 16 in (40 cm). They are elongate, with a broad, blunt head and small, dorsally situated eyes; a dense fringe of cirri bordering the lips; a scaled body; a single dorsal fin without spines; very deep pectoral fins, and widely separated pelvic fins.

A blue cod (*Parapercis colias*) near Fiordland, New Zealand. (Photo by Michael Patrick O'Neill/Photo Researchers, Inc. Reproduced by permission.)

A spotted sanddiver (*Trichonotus setiger*) dives head first under the sand at the first sign of danger. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

Percophids, the duckbills or flatheads, are small, reaching 12 in (30 cm), and elongate; most have a depressed head, large eyes, a scaled body, and two dorsal fins, the first with two to six spines that can be very elongate in some species. Pholidichthyids, the convict blennies, are eel-shaped and grow to 18 in (45 cm), with a rounded head, a single nostril, a scaleless body, spineless long dorsal and anal fins that are continuous with the caudal fin, and reduced pelvic fins. Pinguipedids, the sandperches, are mostly elongate and grow to about 12 in (30 cm). They have an almost cylindrical and scaled body; a single dorsal fin with a shorter, spinous anterior portion; and large pelvic fins. Trachinids, the weeverfishes, are elongate, growing to 17 in (42 cm), with a large oblique mouth (fringed in one species), eyes situated dorsally, and a strong opercular spine with a venom gland. There are two dorsal fins; the first has five to eight strong spines, each bearing a venom gland, and the second is long and directly opposed to the equally long anal fin. The pectoral fins are large, and there are small ctenoid scales in oblique rows along the body.

Trichodontids, the sandfishes, are superficially similar to trachinids. They reach 11.8 in (30 cm), but they are scaleless and have spines on the preopercle rather than the opercle and a longer first dorsal fin with 10–15 spines. Their lips are fringed. Trichonotids, the sanddivers, have a scientific name similar to that of the previous family, which might cause confusion. They are very different fishes, in that they are very elongate and cylindrical, growing to only about 6 in (16 cm). They have a dorsal iris flap with narrow extensions resembling eyelashes, a lower jaw with a fleshy extension beyond the upper jaw, a single long dorsal fin with three to eight anterior spines that are elongate and filamentous in males of some species, fanlike pelvic fins that are larger than the pectoral fins, and a scaled body.

The protruding lower jaws or snouts of this and several other of the sanddiving families presumably facilitate substrate penetration. Uranoscopids, the stargazers, are so named because the eyes are on the top of the head and directed dorsally, looking skyward in typical species. Stargazers, which reach 30 in (75 cm) have a squarish, bulldog-like head en-

cased in sculptured bones, with an almost vertical mouth having fringed lips, a heavy body with or without scales, and a prominent cleithral spine (putatively with a venom gland) just dorsal to the pectoral fin. These fishes have a single dorsal fin with up to four rudimentary spines or two dorsal fins, the first having four to five weak spines, and very large rectangular and fleshy pectoral fins. Some species have a wormlike appendage extending from the respiratory valve of the lower jaw, which is used as "bait" and some have electric organs derived from modified eye muscles, which are reported to be capable of producing 50 volts.

The color pattern varies considerably among trachinoids. Often they are pale or silvery, and they may have bars, saddles, and spots, sometimes with dark markings on the dorsal and caudal fins. Species of some families (e.g., pinguipedids, percophids, and trichonotids) exhibit sexual dichromatism as well as dimorphism. Chiasmodontids, like most bathypelagic fishes, are dark brown or black.

Distribution

Ammodytidae are cold to tropical marine fish found in the Arctic, Atlantic, Indian, and Pacific Oceans and the Black, Mediterranean, and Red Seas. Champsodontidae is a marine family of the Indo-Pacific. Cheimarrichthyidae live in freshwater streams of New Zealand; the larvae are marine. Chiasmodontidae are oceanic marine fishes found in the Atlantic, Indian, and Pacific Oceans. Creediidae is an Indo-West Pacific marine fish. Leptoscopidae are marine fishes found near coastal Australia and New Zealand. Percophidae are marine fishes of the Atlantic, Indian, and Pacific Oceans and the Red Sea. Pholidichthyidae are marine fishes of the Indo-West Pacific, found from coastal Philippines to northern Australia. Pinguipedidae inhabit the Atlantic, Indian, and Pacific Oceans. Trachinidae are marine fishes distributed in the northeastern Atlantic Ocean and the Mediterranean and Black Seas. Trichodontidae are found in the northern Pacific Ocean. Trichonotidae is a marine family of the Indo-West Pacific. Uranoscopidae inhabit the Atlantic, Indian, and Pacific Oceans and the Black, Mediterranean, and Red Seas. Within many of these families, particular genera and species have much more restricted distributions.

Habitat

Most species are marine inshore fishes of tropical to cold temperate regions and are associated in some way with sandy to muddy substrate—sitting on it, in it, or hovering near it to dive for protection when threatened. Exceptions include the Pholidichthyidae, which live in burrows excavated under coral; the Cheimarrichthyidae, which hug the bottom of fast-flowing portions of freshwater streams; the Champsodontidae, which can be found as deep as 3,600 ft (1,100 m) and form large shoals that rise to the surface at night; and the Chiasmodontidae, which are oceanic bathypelagic fishes found almost to 9,500 ft (2,900 m). Even uranoscopids can be found as deep as 2,300 ft (700 m) and percophids to at least 1,970 ft (600 m). Leptoscopids and uranoscopids are the only families with species that normally are found in estuaries as adults.

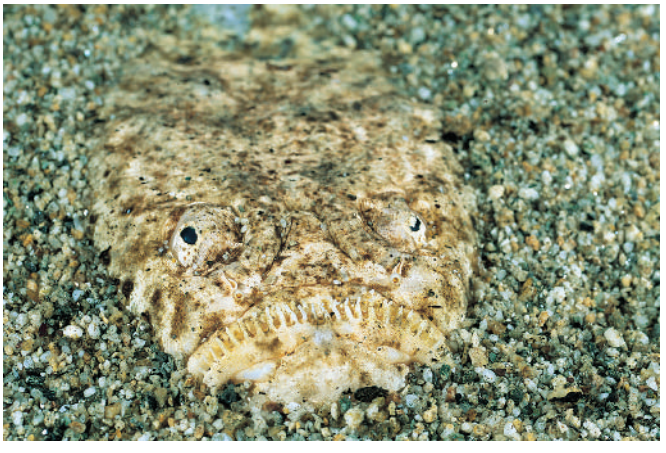
Behavior

Most trachinoids are solitary or form loose aggregations in appropriate habitat. Ammodytids are an exception, often forming dense schools ranging from hundreds to several thousand individuals. Champsodontids also occur in large shoals. Only pinguipedids are known to be territorial. For example, *Parapercis cylindrica* is a protogynous hermaphrodite and polygynous, defending a territory of about 180 ft^2 (17 m^2), within which two to five females defend smaller areas. Male trichonotids have been observed displaying to each other using their long, filamentous dorsal fin spines. It is likely that hemerocoetine percophids, which also have elongated anterior dorsal fin spines, display in a similar manner. Several families have species that exhibit dichromatism and dimorphism, which suggests that display plays a role in communication between or among the sexes.

The activity of ammodytids is related to tidal currents and light levels; they avoid strong tidal currents and are diurnal feeders. At night they hide in sandy substrate and form large shoals during daylight hours and low current and tidal periods. European species are known to bury in the bottom during the low light intensity of northern winters. In contrast, uranoscopids and trachinids apparently move about more at night. Champsodontids exhibit diel movements, moving from the depths to the surface at night. Cheimarrichthyids may migrate to spawn, with females moving from the upper reaches to the lower reaches, where the males are, in summer or autumn. It has been suggested that some species of ammodytids migrate inshore for summer and offshore for winter months. Trichodontids move to shallow rocky shores to spawn, returning to deeper waters after the eggs are laid.

Feeding ecology and diet

All trachinoids are carnivorous, and most are piscivorous, or at least include fishes in the diet. Ammodytids and some of the smaller trachinoid families, such as Trichonotidae, feed on zooplankton or small crustaceans. Pinguipedids feed principally on small benthic crustaceans, and leptoscopids include marine worms in the diet. Uranoscopids, leptoscopids, creediids,



A well-camouflaged marbled stargazer (*Uranoscopus bicinctus*) lies in wait for small fish. (Photo by David Hall/Photo Researchers. Reproduced by permission.)

Two male trichonotids display to each other with their fins erect. (Illustration by Barbara Duperron)

trichonotids, and perhaps trachinids and trichodontids are sit-and-wait predators, hiding in the substrate with only the lips, the top of the head, and the eyes protruding, sucking in unsuspecting fishes and other prey.

Several families that burrow in sand have vertical mouths to facilitate upward attack and fringed lips and gill openings that are thought to prevent sand from entering their mouths and gills while they wait for prey. Uranoscopids also have nasal passages opening into the mouth cavity (which is highly unusual in fishes), permitting them to breathe without opening the mouth while buried. Some have a worm-like appendage inside the mouth that they use as a lure. One genus, *Astroscopus*, has modified eye muscles that can produce an electric shock that might be used to stun prey, though it might instead ward off predators. Pinguipedids and percophids rest on the bottom and chase down prey that is on or near the substrate. Ammodytids forage in the water column. Juvenile pholidichthyids leave their burrows in swarms to feed on plankton during the daytime, streaming back into their tunnels each night to join their parents. The adults have never been observed to leave the burrows, and their diet remains unknown. Chiasmodontids alternate from a chase-and-grab to a floating-trap mode of feeding. They have very large teeth and an extensible stomach to hold on to and eat almost any prey item that they might run across in the relatively food-scarce bathypelagic habitat.

Reproductive biology

Courtship and mating information is scant for most trachinoids. All studied members of the pinguipedid genus *Parapercis* are protogynous hermaphrodites, and at least some are territorial and have harems. Males exhibit head bobbing and pectoral fanning of harem females beginning about 40 minutes before sunset. This behavior culminates in a short ascent from the bottom (less than about 3 ft, or 1 m) for spawning within half an hour after sunset. The genus spawns year-round, with peak activity in summer, a pattern characteristic of tropical species in general and likely the case for tropical representatives of other trachinoid families.

Ammodytids spawn demersal, adhesive eggs, forming clumps on sand or gravel substrate in shallow water. Eggs are not quite spherical and are small, about 0.04 in (1 mm). Females produce 1,800–22,000 eggs, which take from two to 13 weeks to hatch pelagic larvae that are 0.12–0.18 in (3–4.5 mm) long. Most ammodytid species spawn in fall and winter,

though some European species spawn in spring. Trichodontids spawn in winter, producing 600–2,300 eggs in a gelatinous mass attached to either rocks or seaweed, depending on the species. Eggs are relatively large, about 0.14 in (3.5 mm), and yellow, taking from two months to one year to hatch large, pelagic larvae, about 0.6 in (15 mm). Cheimarrichthyids produce up to 30,000 small (about 0.02 in, or 0.6 mm), demersal eggs in rivers during late summer and fall; upon hatching larvae go to sea as part of a pelagic stage.

Champsodontids, chiasmodontids, creediids, leptoscopids, pinguipedids, and trachinids probably are broadcast spawners and produce unornamented, small (< 0.06 in, or 1.5 mm), pelagic eggs, with most shore species hatching in two to six days. The newly hatched pelagic larvae are 0.08–0.18 in (2–4.5 mm) long. Uranoscopids also have pelagic eggs, but they are unusually large (up to 0.1 in, or 2.5 mm); at least some are ornamented with a polygonal network, perhaps helping to maintain the eggs in the water column. Both trachinids and northern representatives of uranoscopids spawn in the spring and summer. Eggs are unknown for the Percophidae, Pholidichthyidae, and Trichonotidae.

Trachinoid larvae can be quite distinctive. Most chiasmodontid larvae bear tiny spicules, whereas one genus, *Kali*, has a unique "gargaropteron" stage, with a large head, oversized pectoral and pelvic fins, and no spicules. Champsodontid larvae have extensive head spination and bear an elongate and narrow opercular appendage that can be as much as 40% of the body length, until it gradually shortens and is resorbed by the time the fish grows to about 0.4 in (10 mm). At least one species of trachinids, *Echiichthys vipera*, has large preopercular spines and large, heavily pigmented pelvic fins. Pholidichthyid larvae and small juveniles (less than 12 in, or 30 cm) are strikingly colored with black and white stripes. They live in burrows with the parents at night, where they attach to the ceiling and hang motionless from mucous strands secreted by the four glands on top of their heads.

Conservation status

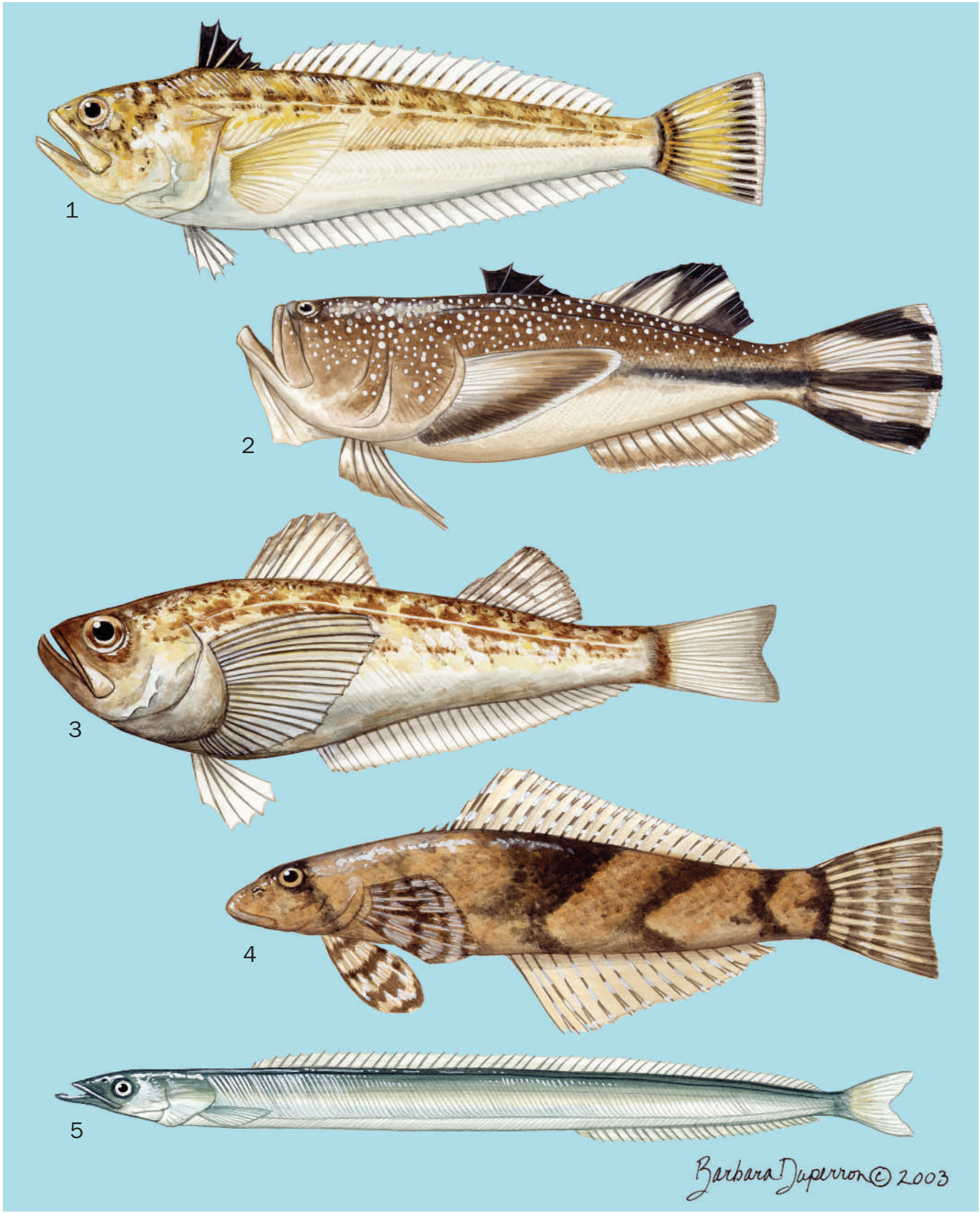
Several species and even families have restricted ranges and exhibit considerable endemism. Many species within families are considered common, in that they are encountered frequently, but population estimates are unknown, except for some species of ammodytids. Although several species are known only from a few specimens, this is generally thought to be due to collecting artifact (difficulty of surveying habitats and so forth) rather than necessarily reflecting actual rarity. No trachinoids are considered endangered, although populations of ammodytids and the trichodontid *Arctoscopus* are monitored because of their commercial importance. The latter experienced overfishing in parts of Japan and had not recovered by 2000.

Significance to humans

Only a few trachinoids are targets for fisheries. Ammodytids are the basis of an important fishery in the North Sea and Japan. Total catch for the multinational North Sea fishery averaged almost 937,000 tons (850,000 metric tons) per year over the years 1996–2000, but this figure fluctuated quite widely and has been more than one million tonnes in a single season. This is an industrial fishery producing fishmeal and oil. Ammodytids are a food fish in Japan, marketed fresh or dried, averaging about 110,000 tons (100,000 metric tons) per year from 1995 to 1999. There is no major fishery for ammodytids in North America, though a minor bait fishery exists in New England, landing only about 22 tons (20 metric tons).

In addition, ammodytids have an indirect impact on humans, as they are important forage fish for seabirds, marine mammals, and other fishes, acting as intermediaries in the food chain by feeding on zooplankton and providing energy to higher predators. Fluctuations in seabird populations in the North Sea appear to be correlated with changes in ammodytid availability, and the abundance of sand lances as a forage fish has implications for such fishery species as mackerel and yellowtail flounder. Similarly, champsodontids are thought to be important forage fishes for commercial species. The dry, but tasty flesh of the greater weever (*Trachinus draco*) is esteemed highly in southern Europe, where it is taken commercially in small quantities; the venomous glands of its spines apparently have discouraged a large fishery. The trichodontid *Arctoscopus japonicus* supports an important commercial fishery as a food fish in Japan. Colloquially, the Japanese name is *kaminarino*, the "thunderfish," referring to its appearance inshore for spawning in late November, when thunderstorms are a common phenomenon in the northern areas where it occurs.

It has been suggested that the common name of the Trachinidae, weeverfishes, derives from the Anglo-Saxon word *wivere*, meaning "viper." Their severe toxicity has been known for at least 2,400 years, since the time of Apollodorus of Alexandria, who is said to have written a book on stinging and biting animals. Modern study has shown that trachinids have grooved opercular and dorsal fin spines bearing venom glands that cause severe pain and occasionally fever, vomiting, and heart failure. Shrimpers sometimes trap trachinids as by-catch and need to handle them with care. Uranoscopids also should be avoided, as they have stout cleithral spines used with good effect for protection. These spines, too, have been reported to be associated with venom glands, but some modern researchers suggest that this association needs to be reappraised. Some uranoscopids also have electric organs and so should be treated with respect. Because members of these two families bury themselves in the sand in shallow water, they are of concern for beachgoers and swimmers, who might tread on them.



1. Lesser weever (*Echiichthys vipera*); 2. Northern stargazer (*Astroscopus guttatus*); 3. Sailfin sandfish (*Arctoscopus japonicus*); 4. Torrentfish (*Cheimarrichthys fosteri*); 5. Inshore sand lance (*Ammodytes americanus*). (Illustration by Barbara Duperron)

Species accounts

Inshore sand lance
Ammodytes americanus

FAMILY
Ammodytidae

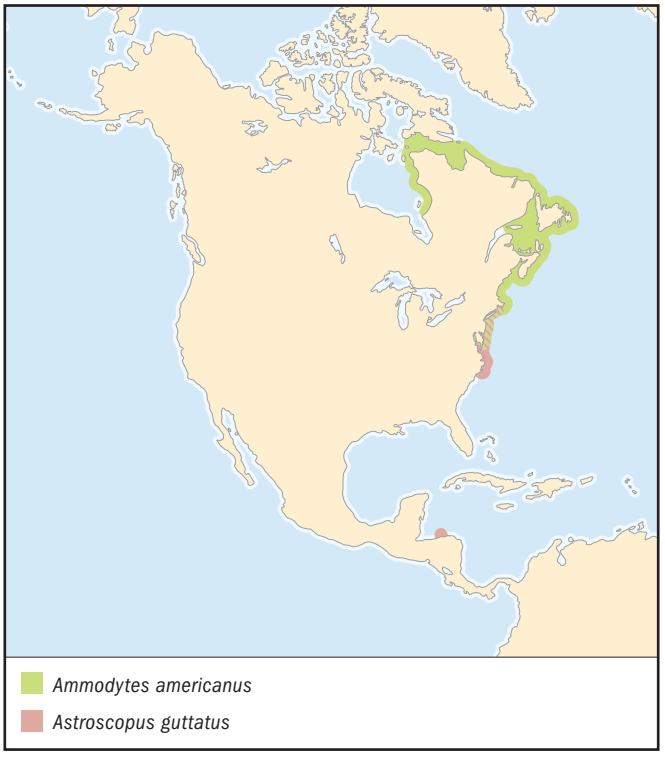
TAXONOMY
Ammodytes americanus DeKay, 1842, Stratford, Connecticut, United States.

OTHER COMMON NAMES
English: American sand lance, sand eel, lance.

PHYSICAL CHARACTERISTICS
Slender and elongate, with a long head and sharply pointed snout and a large, toothless mouth, with the lower jaw projecting far beyond the upper. Long and spineless dorsal fin with 52–61 segmented rays, long and spineless anal fin with 26–33 segmented rays, and forked caudal fin. Has 106–126 (usually 112–124) oblique folds of skin called plicae with cycloid scales underlying them and 63–71 vertebrae (usually 65–70). Coloring is olive, brownish, or bluish green above, with silvery sides and a white belly; some have a longitudinal stripe of iridescent steel blue along each side. Grows to 6.3 in (16 cm).

DISTRIBUTION
Atlantic coast of North America from as far south as Chesapeake Bay (perhaps Cape Hatteras) to Newfoundland and northern Labrador.

HABITAT
Usually shallow water (< 6.5 ft, or 2 m) in estuaries or along coasts over sand or fine gravel substrates used for burrowing.



BEHAVIOR
Form schools of up to several thousand individuals, usually of similar-sized fishes. At high tide they may burrow into the sand and remain on exposed flats until the next tide. Daily movements are not known, and burying behavior, rather than offshore/inshore movements, might explain their sudden appearances and disappearances. It is thought that they spend a good deal of their time buried in the substrate, particularly at night and in the winter.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, especially copepods but also mysids, euphausids, chaetognaths, salps, urochordates, eggs, dinoflagellates, diatoms, and fish fry. Little is known about feeding ecology; even the times and places they feed are the subject of controversy. Inshore sand lances as well as other sand lance species are an important forage species for larger fishes, marine birds, and mammals; they act as agents of energy transfer in the food chain, from zooplankton to higher level predators.

REPRODUCTIVE BIOLOGY
Spawning has not been observed, but it occurs during fall and winter, peaking in December and January and ending in March, probably near shore, where current speeds are low. Most reach reproductive age at the end of their second year, with females' egg production estimated at 1,800–5,200 eggs each season. (Related species have been estimated to produce more than 20,000 eggs.) Eggs are demersal and hatch pelagic larvae after 30–74 days, depending on water temperature. Maximum life span is about 12 years.

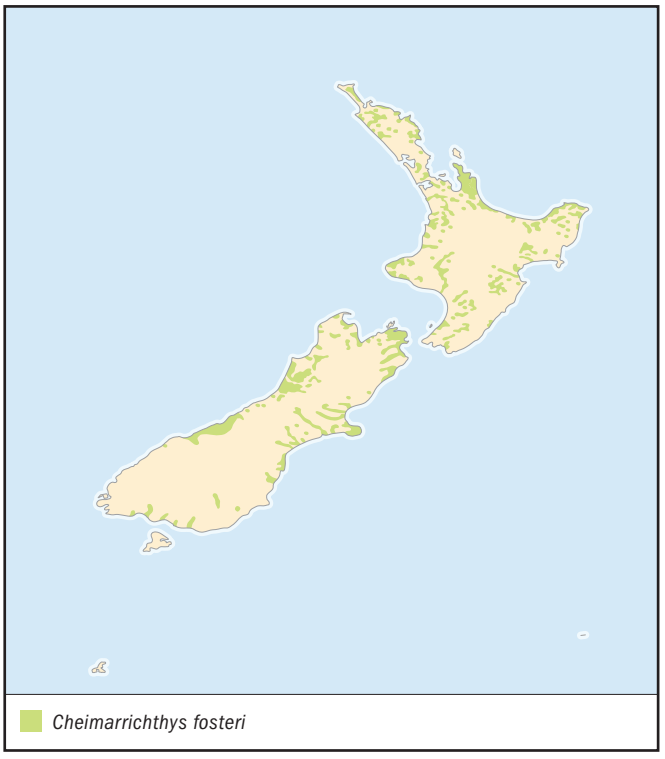
CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
There is little direct significance to humans, with only occasional use in the bait-fish industry. Historical landings are up to 75 metric tonnes per year, though usually well below this amount. They are of great ecological importance and play a significant role as forage fish for at least 20 commercial species including mackerel, herring, cod, hake, pollock, Atlantic salmon, and several flatfish species. Sand lances are also substantial components in the diet of some seabirds (such as terns and cormorants) and marine mammals (such as fin and humpback whales, porpoises, and seals) whose presence impacts tourism. ◆

Torrentfish
Cheimarrichthys fosteri

FAMILY
Cheimarrichthyidae

TAXONOMY
Cheimarrichthys fosteri Haast, 1874, Otira River, New Zealand. Placed in its own family or considered a member of the Pinguipedidae. The latter placement is based on general similarity; the only cladistic studies provide no evidence of a close relationship of *Cheimarrichthys* and pinguipedids.



OTHER COMMON NAMES
Maori: Papanoko.

PHYSICAL CHARACTERISTICS
A broad, somewhat flattened, wedge-shaped head; subterminal mouth; and robust, scaled body. The dorsal fin has three to five short spines and 18–21 segmented rays; the anal fin has one or two spines and 14–16 segmented rays. The pectoral and pelvic fins are large, with about 50 lateral line scales. Grows to 8 in (20 cm).

DISTRIBUTION
Endemic to New Zealand.

HABITAT
Gravel-bottomed rivers in swift riffles from sea level to 2,300 ft (700 m) in elevation and almost 180 mi (300 km) from the sea.

BEHAVIOR
Females occupy areas upstream and males the lower reaches. Diadromous, with juveniles returning from the sea in spring and summer, when they have grown to 0.6–0.8 in (16–20 mm) and are already fully benthic.

FEEDING ECOLOGY AND DIET
Eats slow-moving benthic aquatic insects, especially midges, beetles, and caddis flies, which it probably grazes from cobble/boulder substrates. Thought to move at night from riffles to pools to feed.

REPRODUCTIVE BIOLOGY
It is suggested that females migrate downstream for spawning in summer/autumn, although spawning sites and behavior are unknown. Estimated to lay up to 30,000 small eggs, 0.02 in (0.6 mm) in diameter, that probably sink into the substrate, with larvae developing at sea.

CONSERVATION STATUS
Not threatened, though upstream migration is disrupted easily by man-made structures such as dams.

SIGNIFICANCE TO HUMANS
Of traditional importance to the Maori, but subject to no present utilization. ◆

Lesser weever
Echiichthys vipera

FAMILY
Trachinidae

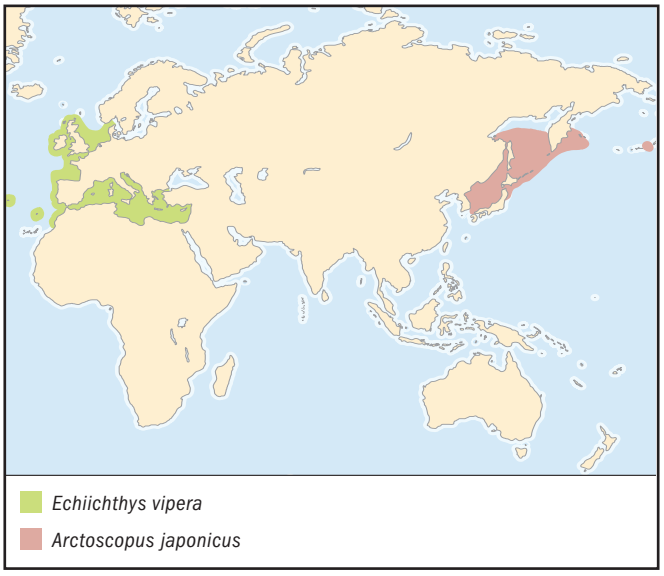
TAXONOMY
Echiichthys vipera Cuvier, 1829, northern England. Originally described as *Trachinus vipera* but given its own genus in 1861 by Bleeker.

OTHER COMMON NAMES
English: Lesser weeverfish, adder pike, black fin, little weever.

PHYSICAL CHARACTERISTICS
Small, elongate, and compressed, with a large, oblique mouth; small, dorsally placed eyes; and a strong, grooved opercular spine bearing a venom gland. Two dorsal fins, the first with five to eight strong spines with anterolateral grooves bearing venom glands and the second long and directly opposed to the anal fin. Distinguished from other family members by fringed lips, a second dorsal fin with 21–24 segmented rays, an anal fin with one spine and 24–26 segmented rays, and rounded pectoral fins. Has about 60 lateral line scales. Coloring is brown dorsally, mottled with darker spots, and pale ventrally. The first dorsal fin is black; the caudal fin is pale with a dusky tip. Grows to 6 in (15 cm).

DISTRIBUTION
Eastern North Atlantic Ocean, including the Azores, and the Mediterranean Sea.

HABITAT
Inshore on sand, mud, or gravel, to 500 ft (150 m), in winter.



BEHAVIOR
During the day hides buried in substrate, with only the eyes and first dorsal fin exposed; becomes more active at night, when it feeds.

FEEDING ECOLOGY AND DIET
Feeds chiefly on crustaceans and fishes.

REPRODUCTIVE BIOLOGY
Breeds June to August, spawning planktonic eggs 0.04–0.06 in (1–1.4 mm) in diameter.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Because of the venomous spines and its inshore, bottom-dwelling habits, it poses a hazard to swimmers. Shrimp fishermen sometimes capture them in their nets and need to handle them carefully. This species is too small for commercial fishery and is taken mostly as incidental catch. ◆

Sailfin sandfish
Arctoscopus japonicus

FAMILY
Trichodontidae

TAXONOMY
Arctoscopus japonicus Steindachner, 1881, Strietok, Sea of Japan, and, questionably, Sitka, Alaska. Originally described as *Trichodon japonicus* by Steindachner, but placed in its own genus by Jordan and Evermann (1896) to emphasize the differences from the only other species in the family, *T. trichodon*.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Compressed, wedge-shaped fishes, with an upturned mouth, fringed lips, spines on the preopercle, and a scaleless body. Two widely spaced dorsal fins, the first having eight to 14 spines and the second having 12–15 segmented rays. Spineless anal fin, with 29–32 segmented rays, and large pectoral fins. Brown mottling dorsally, pale or silvery ventrally, dark bands on both dorsal fins. Grows to 7 in (17 cm).

DISTRIBUTION
Korea to the Sea of Japan, Sea of Okhotsk, and the Bering Sea to Alaska.

HABITAT
Sandy-mud bottom at 650–1,300 ft (200–400 m), sitting on or in the substrate.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Not known; perhaps a sit-and-wait predator or, similarly to trachinids, hides in substrate during the day and is active at night. Feeds primarily on mysids, crangonids, and small fishes.

REPRODUCTIVE BIOLOGY
During November and December there is a conspicuous spawning migration from deeper water to areas of seaweed at 6–33 ft (2–10 m). Eggs, which are about 0.14 in (3.5 mm), are stuck onto *Sargassum* species in spherical masses of about 600–2,300; they hatch asynchronously in about two months. Juveniles school and spend about three months in shallow water before moving into deeper water.

CONSERVATION STATUS
Fisheries in parts of northern Japan collapsed in the early 1980s. Record catches in the late 1960s reached 20,000 tons and held at about 15,000 tons until the late 1970s. By 1984 the catch had plummeted to just 74 tons. A moratorium on fishing was enforced from September 1992 to September 1995, and fishing began again during the spawning season of 1995, but catches remained below 1000 tons up to 1999.

SIGNIFICANCE TO HUMANS
An important food fish in northern Japan, caught by trawl net, set net, and dragnet as the fish come inshore to breed. They are eaten fresh or stored pickled in a mixture of salt and yeast for later consumption. The eggs, called *buriko*, also are eaten, particularly at the New Year. When catches were plentiful, excess fish were dried and used as fertilizer. ◆

Northern stargazer
Astroscopus guttatus

FAMILY
Uranoscopidae

TAXONOMY
Astroscopus guttatus Abbott, 1860, Cape May, New Jersey.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Squarish head with flattened dorsal surface and large, vertical mouth with fringed lips lacking the worm-like appendage characteristic of some other species. Eyes situated dorsally and robust and scaled body. Two dorsal fins, the first with four to five spines and the second with 13–15 segmented rays; anal fin with one spine and 12 segmented rays. Large pectoral fins and cleithral spine just dorsal of the pectoral fin. Small, irregular, white spots on dark background dorsally and gray ventrally with obscure blotches. First dorsal fin dark, second dorsal fin with several distinct oblique bars, caudal fin with alternating black and white stripes, and pectoral fin dark with a pale margin. Grows to 22 in (56 cm) and 20 lb (9.1 kg). Has electric organs modified from the eye muscles in pouches behind the eyes reported to produce up to 50 volts.

DISTRIBUTION
Eastern coast of North America from New York south to North Carolina. One report as far south as Honduras.

HABITAT
Sandy substrate in coastal waters to 130 ft (40 m).

BEHAVIOR
Benthic, spending most of its time buried in the substrate.

FEEDING ECOLOGY AND DIET
A sit-and-wait predator that lies buried on the bottom, with only the top of the head, eyes, and mouth exposed, waiting for small fishes or crustaceans. Lunges at prey aggressively and sucks prey into the large mouth.

REPRODUCTIVE BIOLOGY

Spawns in spring and summer on the bottom, producing pelagic eggs. Larvae are pelagic, settling on sandy bottoms of inshore bays at about 0.6 in (15 mm), remaining there until they grow to 8–12 in (20–30 cm), when they move further offshore.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

Of no commercial or recreational value. When caught, it should be handled with care, owing to the sharp, possibly venomous cleithral spine and the electric organs. ◆

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Randall D. Mooi, PhD
G. David Johnson, PhD

Blennioidei
(Blennies)

Class Actinopterygii
Order Perciformes
Suborder Blennioidei
Number of families 6

Photo: A mimic blenny (*Aspidontus taeniatus*) peers out from a wormhole in coral near the Florida Islands, Solomon Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The suborder Blennioidei has a long and convoluted history of classification, with a variety of families historically being moved into and out of the suborder. Stability finally was established for the suborder when Springer defined the Blennioidei as a monophyletic suborder (i.e., a taxon that includes all the evolutionary descendents, and only those descendents, of a common ancestor). Although the composition of the suborder has been established, the phylogenetic relationships to other families within the order Perciformes remain elusive.

The members of the six families (Blenniidae, Chaenopsidae, Clinidae, Dactyloscopidae, Labrisomidae, and Tripterygiidae) included in the Blennioidei uniquely share a distinctive shape of the joined pelvic bones; another important character is the absence of the second infrapharyngobranchial bone (PB2) from the dorsal gill arch. Springer documented the absence of the PB2 and described the shape of the joined pelvic bones as "a somewhat bean- or nut-like pod, which is open ventrally, and has a dorsally extending flange anteriorly on each side." In addition to this unusual pelvic shape and the loss of the PB2, several other characters that are rarely found in non-blennioid taxa define the Blennioidei. For example, there are cirri on the eye and often on the nape (absent in Dactyloscopidae), the bases of the pelvic fins are positioned anterior to the bases of the pectoral fins, several hypural bones supporting the caudal fin are fused, the anal fin has fewer than three spines, and all segmented rays are unbranched. Johnson described another character, the lack of a neural spine on the first vertebra, further corroborating that the Blennioidei make up a monophyletic group. Although one or a few of these individual characters occur variously in other families, the combination of more than a few of the many shared specialized characters is not found in non-blennioid families.

Few blennioid fossils have been discovered. The combination of their small size and a predominant occurrence along coastlines exposed to wave action and surge probably contributed to the rarity of blenny fossils. The oldest reported blennioid fossil is a late Eocene blennioid otolith described by Nolf.

As of 2002, there are 127 genera and about 750 recognized species in the Blennioidei. Being small, cryptic fishes, blennioids are frequently difficult to collect and identify. The use of rotenone (a natural plant substance found in the roots of a variety of leguminous plants, which aids in the collection of cryptic fishes) to conduct scientific biodiversity surveys of fishes is resulting in the continuous discovery of previously unknown new species of blennioids. If discoveries of new blennioid taxa continue at the current pace, there ultimately may be 1,000 or more valid species of blennioids.

Physical characteristics

Blennioids exhibit amazing diversity in body shapes. They are typically small fishes, usually less than 4 in (15 cm) in length, with many species growing no longer than 2 in (5 cm). Their slender, elongate bodies are very flexible. Most blennioids (not dactyloscopids) have cirri on the head, particularly over the eyes and often on the nape. The only members of the suborder attaining lengths of more than about 10 in (25 cm) are specimens belonging to one Indo-Pacific genus, *Xiphasia*, which have extremely elongate bodies with a depth of less than 0.8 in (2 cm) but reaching lengths of 21.3 in (54 cm). Body shapes range from short and stout and completely or almost completely scaled to elongate and blunt-headed and entirely lacking scales. Several species in the tube blenny genus *Acanthemblemaria* have enlarged spines adorning their heads. Some of the sand stargazers have flattened heads with eyes

A barnacle blenny (*Acanthemblemaria* sp.) from the eastern Pacific near Costa Rica. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

set on protruding stalks. These fish burrow into the sand with only the stalked eyes sticking out as they lie in wait for unsuspecting prey.

Color patterns vary widely, ranging from drab, camouflaging mottled patterns of brown and tan to brilliant reds, yellows, and iridescent blues. Males and females of many blennioid taxa have extremely different colors and patterns. Historically, these differences sometimes have resulted in males and females of the same species being described as two different species.

Distribution

Blennioids are found in shallow marine, estuarine waters of every continent but rarely in freshwaters. The highest diversity of blennioids is in shallow tropical and temperate waters of the Caribbean, western Atlantic, Indian, and Pacific Oceans. Blennioids have not been found in the Arctic Ocean, but they are present in the shallow coastal waters of every other ocean. There is even one triplefin species known from the coast of Antarctica.

Habitat

Blennioids reside in almost every underwater marine habitat imaginable, and some even climb out of the water onto rocks. They are predominately benthic (a few are secondarily free-swimming) and found on or near coral and rocky reefs, where they live in holes and crevices. Other blennioids may live on the bottom among mangrove roots, in sea grass beds, on oyster reefs, or in sandy areas. Although most species live at depths shallower than 66 ft (20 m) and typically less than 33 ft (10 m), *Bathyblennius anthobolps* is known only from a specimen taken at a depth between 330 and 420 ft (101–128 m). The freshwater blenny, *Salaria fluviatilis*, of northern Africa and southern Europe is one of the few blennioids that lives in freshwater streams and rivers. (Some Omobranchini and *Phenablennius* live in freshwater habitats as well.)

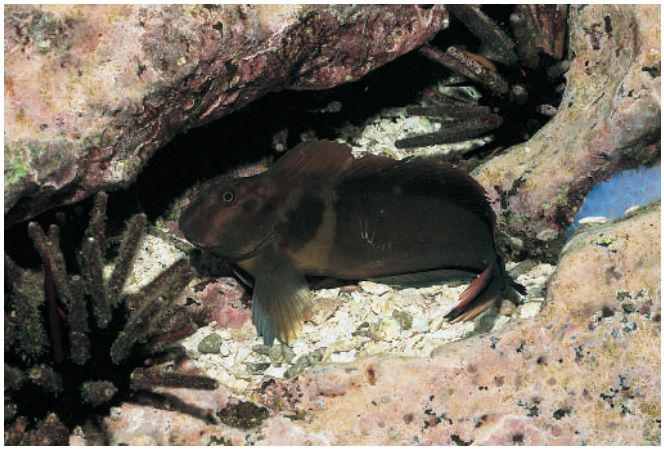
Behavior

Blennioids usually are seen in shallow water, sitting on rocks or coral rubble and using their pelvic fins as props to lift the head off the bottom. They quickly dart into a hole or crevice when approached by a diver. The Indo-Pacific rockhopper blennies of the genera *Alticus* and *Andamia* are found on rocks in high-energy surf zones. The rockhoppers sit just above the waterline and, when threatened, leap from the rock and use quick flicks of the anal and tail fins to skip across the surface of the water to the next emergent rock.

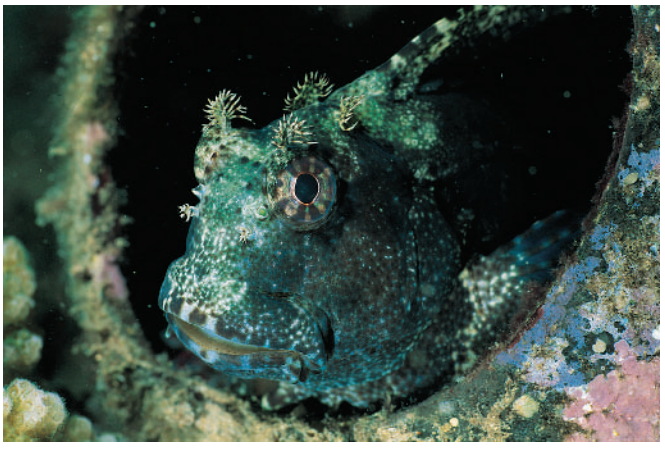
Mimetic associations have been documented for many of the saber-toothed blennies. Mimicry is the process of one species or specimen gaining survival value by changing superficially to resemble another species or specimen. Saber-toothed blennies display previously known types of mimicry, as well as several newly discovered mimetic associations. Batesian mimicry (the most common form) involves a palatable species adapting to resemble an unpalatable species. Müllerian mimicry is defined as two unpalatable species resembling each other. When a predatory and aggressive species resembles a nonagressive species, this is referred to as aggressive mimicry. Social mimicry is seen when two or more species with a similar color pattern swim together in a group for mutual protection.

Feeding ecology and diet

Most blennioids are predatory, eating small benthic invertebrates. The members of the family Blenniidae exhibit a broad range of feeding habits. Some blennies have a row of flexible, comblike teeth used to scrape algae and any associated organisms in the algal mat. Other blennies range in feed-



A large-banded blenny (*Ophioblennius steindachneri*) between two pencil urchins near Caldwell Rock, Galápagos Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)



A jeweled blenny (*Salarias fasciatus*) living in an old coconut shell. (Photo by David Hall/Photo Researchers. Reproduced by permission.)

ing habits from fin ray–eating and membrane-eating aggressive mimics to tube-dwelling plankton pickers. Blennioids are also subject to predation; while the exact predators have not been identified, blennioids are probably eaten by groupers, snappers, and other large piscivores.

Reproductive biology

Reproductive biology is unknown for all but a few blennioids. In the family Blenniidae, males of some species guard and display in front of a small territory, often an empty shell or a rock crevice. The female enters the male's territory; lays large, demersal eggs that adhere to the surface of the shell or rock as they are fertilized by the male; and then leaves. The female sometimes visits two or more males in sequence, repeating the spawning process with each one. The male then guards the eggs and fans water over them until they hatch. Newly hatched fry swim toward the surface and feed on plankton until they settle. The duration of the larval stage varies widely—some blennies settle within a few days of hatching, whereas others may have an extended pelagic larval stage, called the ophioblennius stage, lasting up to one or two months.

The South African, Australian, and Mediterranean members of the Clinidae are ovoviviparous, but the South American members of the family lack an intromittent organ and are oviparous. The tropical eastern Pacific labrisomid genus *Xenomedea* is also ovoviviparous. Males of the labrisomid genus *Starksia* have a distinctive tubular intromittent organ, but live embryos have been found only in a few eastern Pacific *Starksia* species and have not been recorded for any of the Atlantic species.

Conservation status

As of 2002 most populations of marine blennioids were stable, but increasing destruction of coral reefs and coastal pollution are potential threats. The greatest conservation threat to blennioids comes from habitat destruction and pollution. Four species in three families appear on the IUCN Red List—*Entomacrodus cadenati* (Blenniidae) listed as Data Deficient; *Coralliozetus tayrona* (Chaenopsidae) listed as Vulnerable; *Protemblemaria punctata* (Chaenopsidae) listed as Vulnerable; and *Clinus spatulatus* (Clinidae) listed as Endangered. There are no conservation or preservation efforts underway.

Significance to humans

Although blennioids are eaten and can be seen regularly in fish markets from the Philippines to Indonesia and in Peru and Chile in the eastern Pacific, they are not considered commercially important. The primary use of blennioids by humans is as aquarium fish. Specimens of the eastern Pacific blenniid genus *Scartichthys* are consumed in Peru, where eating the flesh supposedly produces a drunken effect. The common name for these fish in Peru is *borracho*, which means "drunk." On Easter Island the Rapa Nui people consider the small patuki blenny to have transformational qualities and associate it with fertility.

1. Blackcheek blenny (*Starksia lepicoelia*); 2. Rosy weedfish (*Heteroclinus roseus*); 3. White-lined comb-tooth blenny (*Ecsenius pictus*); 4. Secretary blenny (*Acanthemblemaria maria*); 5. Sand stargazer (*Dactyloscopus tridigitatus*); 6. Striped poison-fang blenny (*Meiacanthus grammistes*); 7. Hairtail blenny (*Xiphasia setifer*); 8. Miracle triplefin (*Enneapterygius mirabilis*). (Illustration by Patricia Ferrer)

Species accounts

Hairtail blenny
Xiphasia setifer

FAMILY
Blenniidae

TAXONOMY
Xiphasia setifer Swainson, 1839, Vizagapatam, Philippines.

OTHER COMMON NAMES
Japanese: Unagiginpo; South Africa: Slangblennie; Oman and Micronesia: Snakeblenny.

PHYSICAL CHARACTERISTICS
May reach lengths of 23.6 in (60 cm). Large fangs in each jaw but not associated with a toxin gland. Body with alternating bands of dark brown and pale brown. Caudal fin with middle two rays very elongate and forming a hairlike filament and dorsal fin originating above the eye and continuing to the caudal fin. Extremely long and slender body.

DISTRIBUTION
Widely distributed from the western Indian Ocean to the western central Pacific.

HABITAT
Usually found in tubes or burrows in mud or sandy bottoms but may be seen swimming above the bottom or at the surface at night while feeding; shelters in tubes or burrows during the day. Specimens have been captured by trawl at 164–177 ft (50–54 m) off western India.

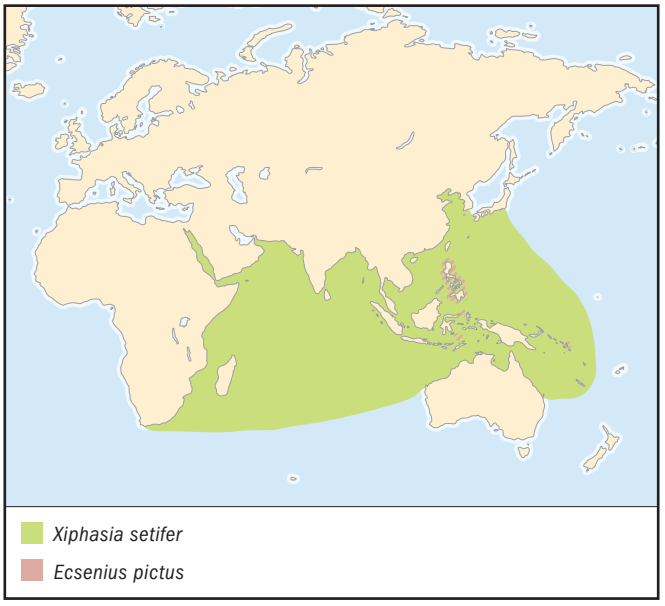
BEHAVIOR
Seldom seen underwater but sometimes attracted to night lights, probably in search of small invertebrates to eat.

FEEDING ECOLOGY AND DIET
Appears to be nocturnal and to forage on small invertebrates.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



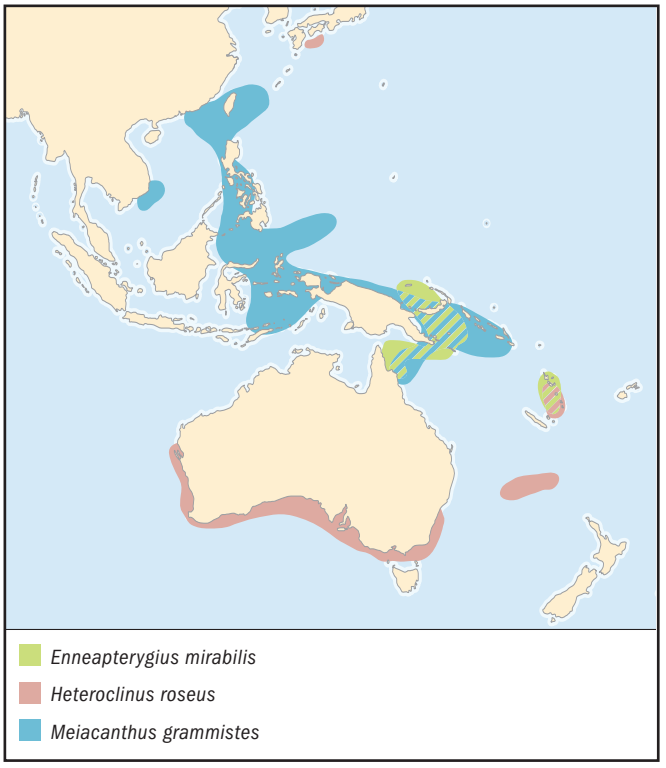
Striped poison-fang blenny
Meiacanthus grammistes

FAMILY
Blenniidae

TAXONOMY
Meiacanthus grammistes Valenciennes in Cuvier and Valenciennes, 1836, Java, Indonesia.

OTHER COMMON NAMES
English: Grammistes blenny; Japanese: Hige-nijiginpo.

PHYSICAL CHARACTERISTICS
May reach lengths of 3.5 in (90 mm). Has a toxin-producing gland enclosed in the dentary at the base of each enlarged, grooved lower-jaw fang. Body has alternating black and white stripes. White stripes are yellowish anteriorly; black stripes are narrow as they approach the base of the caudal fin, where



they break up into small black spots. Caudal fin is translucent, with small black spots; dorsal and anal fins have a black submarginal stripe.

DISTRIBUTION
Widely distributed throughout the western central Pacific from the Ryukyu Islands in the north to the Great Barrier Reef in the south and eastward to the Solomon Islands.

HABITAT
Usually found on or near coral reefs and may be seen swimming above the reef; shelters in tubes or holes in the reef.

BEHAVIOR
This is a venomous species that is able to inject venom using modified fangs in the lower jaw. Unlike most blennies, these fishes have a well-developed swim bladder that allows them to swim easily above the reef. The combination of the swim bladder and their ability to inject venom into a potential predator allows them to swim without restriction above the reef and to forage over a relatively wide area. Like most species of *Meiacanthus*, the striped poison-fang blenny has mimics. Two species are known to be Batesian mimics, a blenniid (*Petroscirtes breviceps*) and a cardinalfish (*Cheilodipterus nigrotaeniatus*). Both of these species swim with the striped poison-fang blenny and avoid predation as a result of potential predators' aversion to the bite of the striped poison-fang blenny.

FEEDING ECOLOGY AND DIET
Forages on small benthic invertebrates on or near the reef.

REPRODUCTIVE BIOLOGY
Unknown but probably similar to that of other blennies. Among other blennies, the male displays to entice one or more females to lay demersal eggs in a hole in the reef, and the male probably guards the eggs until they hatch.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sold as aquarium fish. Potential medicinal uses for substances produced by the venom glands have not been explored. ◆

White-lined comb-tooth blenny
Ecsenius pictus

FAMILY
Blenniidae

TAXONOMY
Ecsenius pictus McKinney and Springer, 1976, Molucca Islands, Indonesia.

OTHER COMMON NAMES
Micronesia: Pictus blenny.

PHYSICAL CHARACTERISTICS
May reach lengths of 2 in (50 mm). Has anterior and posterior canines on each side of the lower jaw and lacks orbital and nape cirri. Body is brown with a series of narrow white stripes ending at the caudal peduncle. The caudal peduncle is yellowish with several brown bands.

DISTRIBUTION
Known to occur only in the western central Pacific in the Philippines, Indonesia, and the Solomon Islands.

HABITAT
Usually found on or near coral reefs at depths of 36–131 ft (11–40 m).

BEHAVIOR
A benthic fish, generally seen perched on coral.

FEEDING ECOLOGY AND DIET
Forages on small benthic invertebrates on or near the reef.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

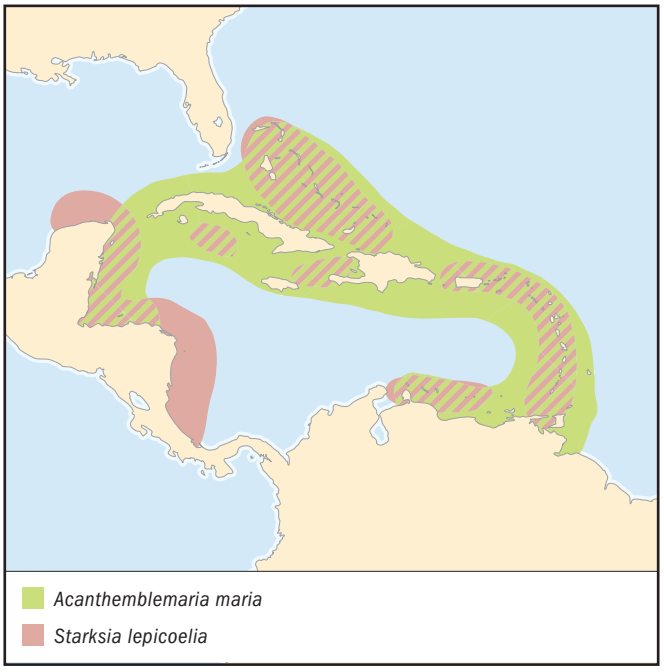
Secretary blenny
Acanthemblemaria maria

FAMILY
Chaenopsidae

TAXONOMY
Acanthemblemaria maria Böhlke, 1961, Treasure Island, Bahamas.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
May reach lengths of 2 in (50 mm). Head has well-developed bony spines covering the top almost to the dorsal



fin origin. Body has broad brown bands separated by narrow pale areas; dark bands sometimes form large oval spots midlaterally.

DISTRIBUTION
Bahamas eastward to Belize and southward to Tobago.

HABITAT
Inhabits small tubes or holes abandoned by tube worms or other invertebrates in rock or limestone slopes and usually is found at depths shallower than 33 ft (10 m).

BEHAVIOR
Generally seen with only the head projecting from a hole, retreating into the hole on the approach of a diver or a large fish.

FEEDING ECOLOGY AND DIET
Feeds on small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Oviparous. Spawning has not been observed but is probably similar to that of other egg-laying blennies.

CONSERVATION STATUS
Not listed by the IUCN. Healthy numbers exist in the western Atlantic and Caribbean. Local populations could be threatened by habitat destruction or pollution.

SIGNIFICANCE TO HUMANS
Potential significance as aquarium fish. ◆

Rosy weedfish
Heteroclinus roseus

FAMILY
Clinidae

TAXONOMY
Heteroclinus roseus Günther, 1861, Freycinets Harbour, Western Australia.

OTHER COMMON NAMES
Japanese: Beni-asahiginpo.

PHYSICAL CHARACTERISTICS
May reach maximum lengths of 5.7 in (145 mm). The rosy weedfish is distinguished from other *Heteroclinus* species by having a black spot, bordered above and below by a white stripe, on the pectoral fin-base.

DISTRIBUTION
Primarily anti-subtropical in distribution, occurring north of approximately 20° N latitude and south of roughly 20° S latitude, and absent in tropical equatorial waters. A northern population occurs in Japan and a disjunct southern population living around the southern half of Australia, Lord Howe Island, Kermadec Islands, New Caledonia, and Vanuatu.

HABITAT
The rosy weedfish lives on rocky reefs from the intertidal zone to depths of 115 ft (35 m).

BEHAVIOR
Rarely seen underwater owing to its very cryptic coloration. Sits on the bottom using its pelvic fins as supports to lift the head.

FEEDING ECOLOGY AND DIET
Predatory, probably feeding on small benthic invertebrates.

REPRODUCTIVE BIOLOGY
The presence of an intromittent organ in males suggests that it (like all other clinids in the Indo-Pacific) is ovoviviparous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Sand stargazer
Dactyloscopus tridigitatus

FAMILY
Dactyloscopidae

TAXONOMY
Dactyloscopus tridigitatus Gill, 1859, Barbados.

OTHER COMMON NAMES
Spanish: Mirón ojilargo.

PHYSICAL CHARACTERISTICS
May reach lengths of 3 in (75 mm). A distinctive Atlantic sand stargazer with the eye perched on a slender stalk on top of the head. It differs from other Atlantic sand stargazers in that it has a tube in the last lateral line scale at the base of the caudal fin.

DISTRIBUTION
Bermuda, northeastern Gulf of Mexico, Bahamas, and the Caribbean as far as Brazil.

HABITAT
Soft, sandy bottoms from shallow water off beaches to depths of 98 ft (30 m).

BEHAVIOR
Burrows into the sand with only the stalked eyes on the top of the head exposed.

FEEDING ECOLOGY AND DIET
It is predatory on small prey, presumably invertebrates, but the sand stargazer has not been observed feeding.

REPRODUCTIVE BIOLOGY
Oviparous. Males and females mature at about 1.8 in (45 mm) in length. Spawning had not been observed as of 2002.

CONSERVATION STATUS
Not listed by the IUCN. Pollution is the biggest potential threat.

SIGNIFICANCE TO HUMANS
None known. ◆

Blackcheek blenny
Starksia lepicoelia

FAMILY
Labrisomidae

TAXONOMY
Starksia lepicoelia Böhlke and Springer, 1961, Green Cay, Bahamas.

OTHER COMMON NAMES
Spanish: Sapito carinegro.

PHYSICAL CHARACTERISTICS
May reach a maximum length of 1.4 in (35 mm). The blackcheek blenny can be distinguished from other Atlantic *Starksia* by the presence of a black spot covering most of the cheek in mature males, a completely scaled belly, and male genital papilla entirely separate from the first anal fin spine.

DISTRIBUTION
May be found on coral reefs from the Bahamas and throughout the Caribbean.

HABITAT
Coral reefs at depths of 26–66 ft (8–20 m).

BEHAVIOR
Secretive and rarely seen underwater.

FEEDING ECOLOGY AND DIET
Predatory on small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Mature females have well-developed ova in the ovaries, and the males have an intromittent organ, but the presence of embryos in a female (viviparity) has not been documented. It seems likely that the species is oviparous, as no gravid female Atlantic blackcheek blenny has ever been found.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Miracle triplefin
Enneapterygius mirabilis

FAMILY
Tripterygiidae

TAXONOMY
Enneapterygius mirabilis Fricke, 1994, Escape Reef, Australia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
May reach lengths of 1.2 in (30 mm). Distinguished from other *Enneapterygius* species by having 12 or fewer tubed scales in the anterior portion of the lateral line and by its long, filamentous spines in the first dorsal fin.

DISTRIBUTION
Known from Papua New Guinea, northern Queensland, Australia, and Vanuatu.

HABITAT
Has been found at depths of 26–121 ft (8–37 m) on coral reefs and adjacent reef slopes.

BEHAVIOR
The miracle triplefin, like so many of the blennioids, has yet to be observed alive underwater. It has been seen and collected only after the application of rotenone, without which this magnificent blenny's existence would be unknown.

FEEDING ECOLOGY AND DIET
The diet is unknown, but the presence of small, sharp, conical teeth in the jaws suggests that the miracle triplefin feeds on small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Oviparous, based on the presence of mature ova in females, but breeding individuals have not been observed, and young are unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not currently used by humans, but its red color and high first dorsal fin make it an attractive species. ◆

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Jeffrey Taylor Williams, PhD

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Icosteoidei
(Ragfish)

Class Actinopterygii
Order Perciformes
Suborder Icosteoidei
Number of families 1

Photo: A ragfish (*Icosteus aenigmaticus*) juvenile. The ragfish transforms as it ages. The juvenile has a spotted color pattern, small pelvic fins, and has spines along its lateral line. As it grows, it changes to a chocolate brown and loses its pelvic fins. (Photo by K. Gus Thiesfeld. Reproduced by permission.)

Evolution and systematics

When the juvenile ragfish was first described by Lockington in 1880, there was apparently a premonition of the difficulty in placing this species into any existing taxonomic groupings. Indeed, the name of the single icosteoid representative, *Icosteus aenigmaticus*, means "puzzling fish with yielding bones." Lockington hypothesized the ragfish's probable relationship to the blennioid fishes. He questionably assigned it to the family Blenniidae (the blennies) but stated that it probably should be in its own family.

In the next twenty years, Lockington's contemporaries offered other taxonomic schemes. In 1881 Steindachner also examined a juvenile ragfish and concluded that it was not a blennioid and should be positioned with *Icichthys* (the medusafish). In 1887 Günther examined two juveniles and proposed a coryphaenid (dolphin) affinity. In 1887 Tarleton H. Bean described the first adult ragfish; being of such dissimilar appearance to the juvenile form, it was recognized as its own species, *Acrotus willoughbyi*, and placed in the family Icosteidae, along with *Icosteus* and *Icichthys*. Several years later *Acrotus* was elevated to its own family, Acrotidae.

The next 70 years yielded few studies of ragfish (actually, ragfishes at this time) systematics. During this period, the ragfish received little attention, doubtless because of its rare occurrence. Most ichthyologists still agreed that it was a percomorph (typical spiny-rayed fishes), though degenerate and specialized. The majority of researchers recognized a stromateoid (medusafish, butterfishes, and squaretails) affinity. A few, such as Berg in 1940, believed that the ragfish should be elevated to its own order, Icosteiformes.

In 1961 Clemens and Wilby observed that *Icosteus* (the fan-tailed ragfish) was the juvenile form of the adult *Acrotus* (the brown ragfish). At that time, interest in the ragfish was renewed, and since then the science of systematics has advanced in the methods of interpreting characteristics that elucidate affinities between groups. Studies on internal anatomy, external morphological features, and early life history have been adding to our knowledge of ragfish. With this information, investigators may be able to piece together the "puzzling" systematic relationships of the ragfish.

The taxonomy for this species is *Icosteus aenigmaticus* Lockington, 1880.

Other common names include ragfish, spotted ragfish, speckled ragfish, fan-tailed ragfish, giant ragfish, and brown ragfish.

Physical characteristics

Juvenile ragfish have limp bodies that are easily doubled over like a wet rag (hence the name ragfish). They are deep-bodied and laterally compressed (especially the region along the dorsal and anal fin base), with a slender caudal peduncle. The body is smooth-skinned and scaleless, except along the lateral line, where the scales produce groups of numerous small spines. The lateral line is minimally arched anteriorlyand then straight. The head is short, with an abrupt, high predorsal profile. The eyes are small. The mouth is terminal, with limited protrusibility. The teeth are minute and comblike. The snout is blunt and has been described as calflike. The dorsal fin has one spine and 52–56 soft rays, and the anal fin has 37–40 soft rays. The caudal fin is rounded and

Ragfish (*Icosteus aenigmaticus*) have cartilage rather than bones, so are limp and "rag-like" when out of the water. They live deep in the water, so it is unusual to see them. The female fish on the left measures 5.05 ft (1.54 m). The male on the right is 5 ft (1.525 m). (Photo by K. Gus Thiesfeld. Reproduced by permission.)

fanlike. The pelvic fins have one spine and four soft rays. All fins have small spinules on the surface. Smaller juveniles (less than 4.7 in, or 120 mm, in length) have mottled dark blotches over a light grayish purple background. Juveniles longer than 4.7 in (120 mm) have numerous irregular spots over a light grayish purple background, which are less prominent along the ventral region of the body.

At 14.2–16.5 in (360–420 mm), ragfish undergo a remarkable transformation into an adult form that is very different from the juvenile form. The body becomes more elongated, and a fleshy keel becomes pronounced along the ventral midline. The lateral line scale spines disappear, and the number of dorsal and anal fin rays decrease as the skin along the anterior origins encroaches on the leading spine and rays. The pelvic fins disappear. The caudal fin margin broadens and becomes emarginate to slightly forked. The spinules on the fins are reabsorbed. Finally, the coloration turns to a uniform dark brown over the entire body and fins.

Ragfish have been reported to reach a length of more than 6.9 ft (2.1 m). Adult males seem to attain the greatest length, while most females grow to about 5 ft (1.6 m). Adult females appear to be deeper bodied and weigh nearly twice as much as a male of similar size.

Distribution

Ragfish are distributed from San Onofre, California, to immediately north of the Aleutian Islands and across the northern Pacific to Kochi City, southeastern Japan. They are considered rare but are less so north of Cape Mendocino, California.

A ragfish (*Icosteus aenigmaticus*) female that measures 48 in (1.2 m). Note the absence of spotted coloration, pelvic fins, and lateral line spines. (Photo by K. Gus Thiesfeld. Reproduced by permission.)

Habitat

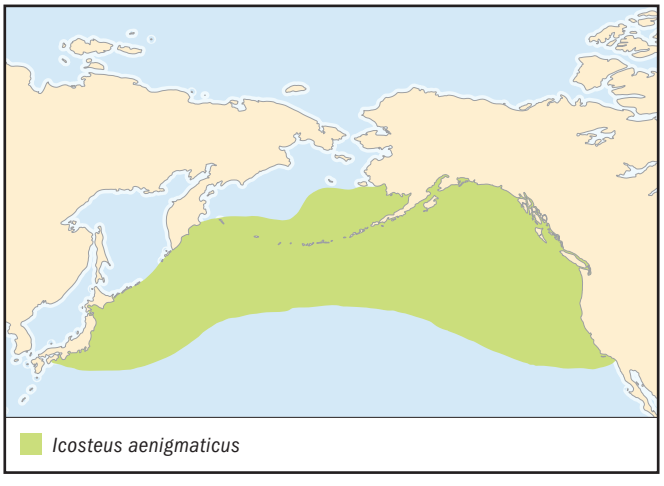
Ragfish are captured from the surface to depths of more than 1,640 ft (500 m). They usually are offshore over deeper water, which suggests an epipelagic or mesopelagic habitat. The juvenile's spotted coloration, however, might imply a benthic habitat.

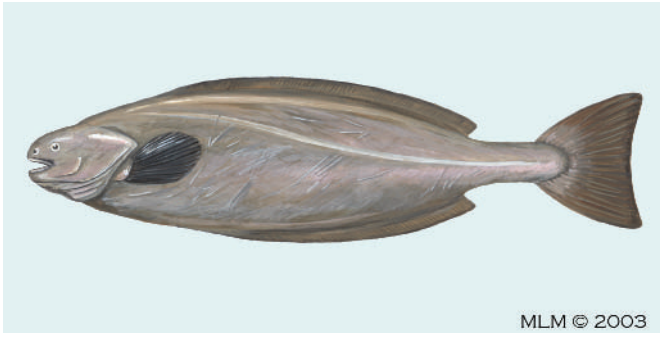
Behavior

There is little information on ragfish behavior. They most likely are not schooling fish, because they always are captured individually. Rarely, large ragfish are found stranded on the shore. Ragfish have never been observed in their natural habitat.

Feeding ecology and diet

Little is known of the feeding ecology of the ragfish. Those that are collected rarely have identifiable food items in the stomach. In 1968 Fitch and Lavenberg reported small fishes, squid, and octopods as possible prey items. There also is evidence of gelativory in ragfish. Gelativory is the consumption of jellyfishes and their relatives. Preliminary investigations of the internal anatomy suggest morphological specializations to accommodate a gelativorous diet.





Ragfish (*Icosteus aenigmaticus*). (Illustration by Michelle Meneghini)

Ragfish probably are preyed upon by piscivorous (fish-eating) fishes. There is one record from Washington of a small juvenile ragfish found in the stomach of a tuna. In 1938 Cowan reported that a colleague identified the adult ragfish as the whaler's "bastard halibut," which forms a large part of the diet of sperm whales taken in deep water off Queen Charlotte Island, British Columbia.

Reproductive biology

Ragfish are oviparous and ready to spawn at seven to nine years of age, according to Fitch and Lavenberg, and they spawn in summer. In 1968 Allen studied four adult females and postulated that spawning occurs in late winter and early spring. Allen observed that eggs were largest (to 0.12 in, or 3.0 mm, in diameter) at that time and estimated fecundity to be 430,000 eggs for a 59-in (1.5-m) female. It is not known whether ragfish undergo spawning migrations or become territorial. Eggs are nonadhesive and planktonic, with a single oil globule. The larvae are distinctly pigmented and planktonic.

Conservation status

This species is not listed by the IUCN.

Significance to humans

Ragfish have no sport or commercial fishing value. They occur rarely in the bycatch of commercial shrimp and bottom fish trawlers.

Resources

Books

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K. Gus Thiesfeld, BS

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Gobiesocoidei
(Clingfishes and singleslits)

Class Actinopterygii
Order Perciformes
Suborder Gobiesocoidei
Number of families 1

Photo: Clingfish (*Lepadichthys lineatus*) use their sucking disc (modified pelvic fins) to cling to rocks, marine plants, or even sea urchins. (Photo by Animals Animals ©W. Gregory Brown. Reproduced by permission.)

Evolution and systematics

No clingfishes and singleslits have been identified from the fossil record, and the evolutionary history remains to be examined with molecular methods. The examination of morphological relationships has led to the formulation of competing hypotheses to describe the history and systematic position of clingfishes and singleslits, and these questions are far from resolved. Some workers place these fishes in the order Gobiesociformes along with the dragonets (Callionymidae) and draconetts (Draconettidae). Others place the Gobiesocidae in the suborder Gobiesocoidei within the Perciformes, next to the suborder Callionymoidei (Callionymidae and Draconettidae); such is the treatment in this chapter.

The family Gobiesocidae is partitioned into two subfamilies, the Gobiesocinae (clingfishes) and the Cheilobranchinae (singleslits) within the Gobiesocoidei. Both subfamilies are united by the presence of a joint that connects the supracleithrum and cleithrum bones within the pelvic girdle. Two other specializations link these two subfamilies: a joint connecting the interopercle and epihyal and a heart with a structure unique to both subfamilies. The singleslits are sometimes recognized as a separate family within the suborder Gobiesocoidei; the family consists of a single genus, *Alabes*, with four species. Briggs recognized the following subfamilies (denoted here as tribes), which now are placed under the Gobiesocinae: the primitive Trachelochismini, the monotypic Haplocylicini, the Lepadogastrini, the monotypic Chorisochismini, the Diplocrepini, the Gobiesocini, and the highly specialized Diademichthyini, which are mostly commensal with sea urchins and crinoids. Briggs concluded that more specialized taxa are found in the tropical Indo-West Pacific region; intermediate taxa are found in the eastern Pacific, western Atlantic, and eastern Atlantic; and relict Southern Hemisphere taxa are confined to the cool temperate waters of southern Africa, Australia, and New Zealand. There are at least 120 species of clingfishes (two with two subspecies each and one with three subspecies) in 44 genera plus undescribed genera and species.

The known genera include *Acyrtops* (two species), *Acyrtus* (two species), *Alabes* (four species), *Apletodon* (four species, one with two subspecies), *Arcos* (five species), *Aspasma* (one species), *Aspasmichthys* (one species), *Aspasmodes* (one species), *Aspasmogaster* (four species), *Chorisochismus* (one species), *Cochleoceps* (four species), *Conidens* (two species), *Creocele* (one species), *Dellichthys* (one species), *Derilissus* (two species), *Diademichthys* (one species), *Diplecogaster* (three species, one with three subspecies), *Discotrema* (one species), *Eckloniaichthys* (one species), *Gastrocyathus* (one species), *Gastrocymba* (one species), *Gastroscyphus* (one species), *Gobiesox* (26 species), *Gouania* (one species), *Haplocylix* (one species), *Kopua* (one species), *Lecanogaster* (one species), *Lepadichthys* (nine species), *Lepadogaster* (three species, one with two subspecies), *Liobranchia* (one species), *Lissonanchus* (one species), *Modicus* (two species), *Opeatogenys* (two species), *Parvicrepis* (one species), *Pherallodichthys* (one species), *Pherallodiscus* (one species), *Pherallodus* (two species), *Posidonichthys* (one species), *Propherallodus* (one species), *Rimicola* (five species), *Sicyases* (two species), *Tomicodon* (13 species), and *Trachelochismus* (two species).

Physical characteristics

The clingfishes are denoted mainly by the presence of pelvic fins modified into a sucking disk. Unlike the gobies (Gobiidae, Perciformes), which possess pelvic fins modified into a suction cup, the clingfishes lack a spinous dorsal fin. With some exceptions, clingfishes are tadpole-like, with broad, depressed heads and flattened bodies. Some species, however, are elongate with pointed snouts. Clingfishes lack scales but shield themselves with a mucus that forms a protective coat around their bodies. The lateral line is well developed anteriorly but is either small or missing posteriorly.

A crinoid clingfish (*Discotrema crinophila*) from Myanmar. (Photo by Animals Animals © Don Brown. Reproduced by permission.)

There is a well-developed network of sensory pores on the head. There is one dorsal and one anal fin.

The sucking disc is of two types: a single disc, in which the anterior and posterior components form a single continuous structure, and a double disc, in which the larger anterior and smaller posterior components form two discs separated by a single wall or edge. The pectoral fins generally are small and are positioned posterior to the sucking disk. The dorsal nostril and, usually, the posterior nostril are both tubular. The swim bladder is absent. Color patterns are variable and range from black to orange, brown, green, or red. Additionally, there may also be contrasting stripes, bars, or spots of yellow, blue, green, brown, gray, or white. The larvae are elongate, torpedo-shaped, and laterally compressed, and they become more rounded with growth. The gas bladder, located above the gut, is present but is lost after settlement. Body sizes typically are small, less than 1.9–2.4 in (5–6 cm) in total length, but at least one temperate species from southern Africa, the rocksucker (*Chorisochismus dentex*), reaches 11.8 in (30 cm). Clingfishes are sexually dimorphic, with differences in the size of the urogenital papillae and also in body size—males generally are larger than females. Two species reportedly produce a skin toxin.

The singleslits are eel-like in shape, with diminutive pelvic fins and a vestigial sucking disc. Their dorsal and anal fins are modified to resemble those of true eels. Soft rays are present only in the caudal fin. The posterior nostril is absent in one species. Color patterns are also variable and range from translucent pink or green to light green, brown, gray, or black. Spots or bars of black, gray, brown, or yellow may also be present. Usually they are less than 1.9 in (5 cm) in length, but one species, the common shore-eel (*Alabes dorsalis*) of Australia, reaches 4.7 in (12 cm).

Distribution

Clingfishes occur in marine and brackish waters in tropical, warm temperate, and temperate zones of the Atlantic, Indian and Pacific Oceans. General distribution patterns may be described best by relying upon Briggs' classification scheme, as modified here. Thus, the Trachelochismini consists of Southern Hemisphere relict species restricted, except for two Northern Hemisphere species, to temperate Australia and New Zealand. The monotypic Haplocylicini is endemic to New Zealand. Members of the Lepadogastrini occur in the eastern Atlantic and Mediterranean Sea, with one species found in deeper waters of southern Africa. The Chorisochismini is monotypic and also is found in southern Africa, but in shallower, warm temperate waters. The Diplocrepini is distributed across the Indo-West Pacific, with one deepwater relict species occurring in the Caribbean. The Gobiesocini occurs in the western Atlantic and eastern Pacific; some also are found in freshwater streams of the Caribbean, Central America, and Cocos Island in the eastern Pacific. One monotypic genus occurs in southern Africa. The Diademichthyini also is found in tropical waters of the Indo-West Pacific region. Singleslits are restricted to temperate inshore waters of the southern Australian mainland, Tasmania, and Norfolk Island.

Habitat

Clingfishes are largely inshore fishes adapted to clinging to the substrate. Thus, they are able to colonize high-energy habitats and withstand breaking waves and surging waters. Many species occur on or under boulders and rocks, in crevices, and on rocky slopes and rock faces. Species adapted to living in tide pools are capable of remaining out of water for a number of days, if they are kept moist and out of sunlight. Other species are found in close association with corals, soft corals, sponges, and ascidians. Some species live among crinoids or sea urchins. The crinoid clingfish, *Discotrema crinophila*, lives secluded among the arms of crinoids. *Diademichthys lineatus* has strayed from the general clingfish body plan by evolving an elongated shape that nearly mimics the long spines of *Diadema* sea urchins. Other species cling to the blades of sea grasses and to seaweed and kelp. Some members of the genus *Gobiesox* occur in freshwater streams. Singleslits also live in inshore marine waters, usually in shallow tide pools and often under stones or in close association with seaweed, the stems or branches of which they may cling to or wrap around with their prehensile caudal fins and flexible bodies.

Behavior

Clingfishes and singleslits tend to be secretive, although the reef-associated species commensal with sea urchins and other organisms are more mobile and swim in the water column. Territoriality has been reported for numerous species and is suspected for the rest. This trait is more pronounced in males. Most observations of other behavioral activity have been confined to aquarium studies; field investigations, where physically possible, are desirable.

Feeding ecology and diet

The clingfishes generally feed on smaller benthic invertebrates, but there are significant exceptions to this rule. Clingfish diets, depending upon species, body size, and habitat,

include various algae, crustaceans (including amphipods, copepods, small crabs and shrimps), polychaete worms, small bivalves, limpets and other gastropods, chitons, body parts of host sea urchins, and small fishes. Members of the genus *Cochleoceps* are cleaner fishes that remove ectoparasites from boxfishes, porcupinefishes, morwongs, and other species. The singleslits feed mainly on small benthic invertebrates. Clingfishes are preyed upon by other fishes, shorebirds, and possibly crabs living in the intertidal zone.

Reproductive biology

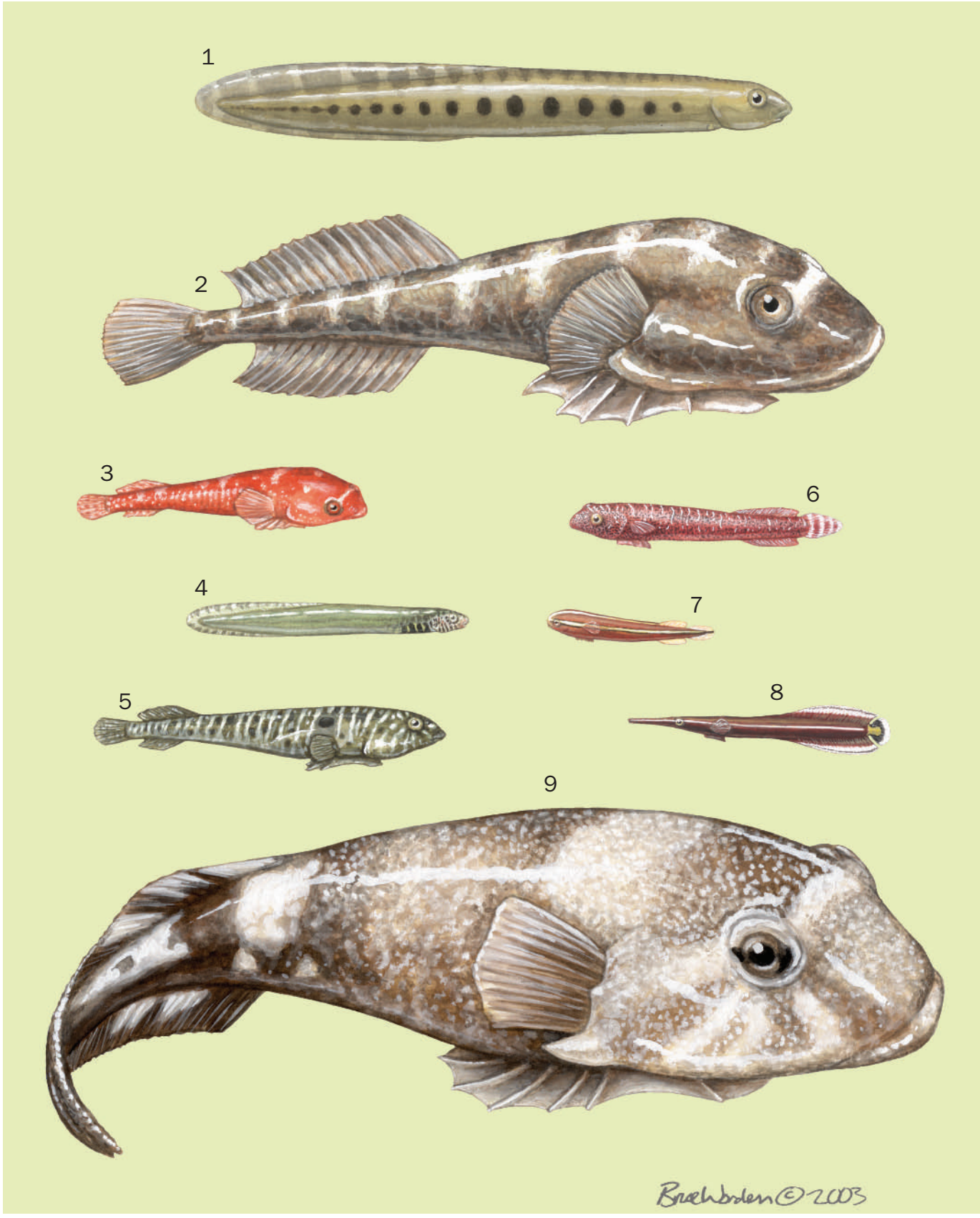
Reproductive behavior and ecology have been described for a number of species, mainly from aquarium studies, and, as expected, there is species-specific variation around a common theme. Courtship is paired and initiated by the male within his territory. Generally, the male nudges the female's abodomen; if the female responds positively, he moves parallel to her flank and undulates or quivers. After some time, the female will undulate her body and lay demersal eggs singly until a small clutch is produced. (Demersal eggs are those that are deposited upon the substrate, such as the sea floor.) Eggs may be laid on stones, algae, or other substrates. Depending upon the species, egg laying may last from several minutes to a few hours. The male fertilizes the eggs during this process, and, upon completion, the clutch either is guarded by the male or is abandoned by the pair. There is some evidence of mating by internal fertilization, with female parental care, in the weedsucker (*Eckloniaichthys scylliorhiniceps*). This species is a monotypic clingfish endemic to South Africa that may share this trait with a few other species. Spawning or mating may be seasonal, during warmer months, at higher latitudes. At tropical or subtropical latitudes, spawning or mating may take place year-round or seasonally if water temperatures become either too warm or too cold. Larvae of all species are probably planktonic.

Conservation status

No species is currently on the IUCN Red List. Marine and freshwater species with limited distributions may be at risk from habitat destruction or pollution.

Significance to humans

Some species are collected for the aquarium trade.



1. Common shore-eel (*Alabes dorsalis*); 2. Northern clingfish (*Gobiesox maeandricus*); 3. Two-spotted clingfish (*Diplecogaster bimaculata bimaculata*); 4. Pygmy shore-eel (*Alabes parvulus*); 5. Sonora clingfish (*Tomicodon humeralis*); 6. Eastern cleaner-clingfish (*Cochleoceps orientalis*); 7. Crinoid clingfish (*Discotrema crinophila*); 8. Urchin clingfish (*Diademichthys lineatus*); 9. Rocksucker (*Chorisochismus dentex*). (Illustration by Bruce Worden)

Species accounts

Common shore-eel
Alabes dorsalis

FAMILY
Gobiesocidae

TAXONOMY
Alabes dorsalis Richardson, 1845, attributed to the northwest coast of Australia, but this is likely a type locality error.

OTHER COMMON NAMES
English: Shore eel.

PHYSICAL CHARACTERISTICS
Body small and elongate (eel-like) with reduced fins. Vestigial sucking disc. Color variously gray to black, with prominent green spots along the flank and gray to black blotches regularly spaced along the dorsal fin. Grows to 4.7 in (12 cm) in length.

DISTRIBUTION
Australia from southern New South Wales south to Tasmania and west to central South Australia.

HABITAT
Intertidal zone under rocks.

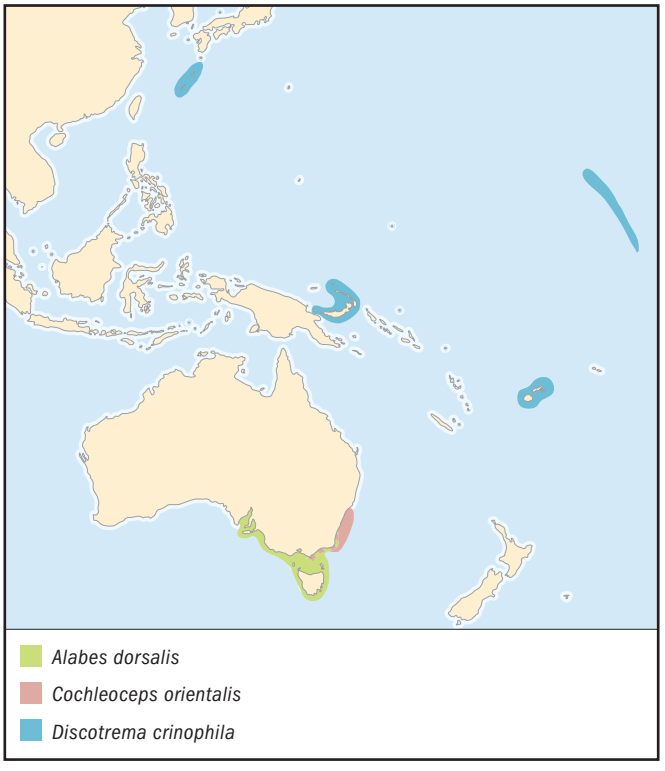
BEHAVIOR
Poorly known. This species is secretive and seldom seen. The common shore-eel moves rather like a true eel among and under rocks, into holes, and along the bottom of tide pools. Nothing is known about its social behavior, although it may be territorial, like others in its family. May tolerate exposure to air during exceptionally low tides.

FEEDING ECOLOGY AND DIET
Feeds upon small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Unknown. Spawning probably is seasonal, during warmer months, and paired with the deposition of demersal eggs. Larvae are probably planktonic.

CONSERVATION STATUS
Not listed by the IUCN. May be at risk from habitat destruction or pollution.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆



Crinoid clingfish
Discotrema crinophila

FAMILY
Gobiesocidae

TAXONOMY
Discotrema crinophila Briggs, 1976, between Stuart and Yanuca islands, Benga Lagoon, Benga, Fiji Islands.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Elongate body, with a rounded snout. There are 8–9 dorsal fin soft rays and 7–8 anal fin soft rays. Color is black, with a yellow stripe that runs along each flank from the snout to the base of the caudal fin and a mid-dorsal yellow stripe that joins the lateral stripes at the snout.

DISTRIBUTION
Western Pacific, from the Ryukyu Islands of southern Japan south to Taiwan, southeast to the Bismarck Archipelago in Papua New Guinea, and east to Fiji and Christmas Island, Line Islands (Kiribati). Specimens reported from the Great Barrier Reef, and possibly the Bismarck Archipelago, represent an undescribed species.

HABITAT
Lives among the arms of crinoids on coral reefs at a depth range of 26–66 ft (8–20 m).

BEHAVIOR
Poorly known. Swims about the arms of crinoids.

FEEDING ECOLOGY AND DIET
Feeds upon small invertebrates.

REPRODUCTIVE BIOLOGY
Poorly known but likely lays demersal eggs, perhaps at the base of a crinoid.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆

Eastern cleaner-clingfish
Cochleoceps orientalis

FAMILY
Gobiesocidae

TAXONOMY
Cochleoceps orientalis Hutchins, 1991, Big Island, off Wollongong, New South Wales, Australia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Small, tadpole-shaped body with rounded caudal fins and a moderately sized sucker disc. There are 5–6 dorsal fin soft rays and 4–6 anal fin soft rays. Color pattern is tiny brown to red spots on an orange to yellow or greenish-yellow background; irridescent blue dashes, lines, or spots occur on the dorsum. Grows to 2.2 in (5.5 cm) in length.

DISTRIBUTION
Southwest Pacific from central New South Wales south to eastern Victoria, Australia.

HABITAT
Occurs on sponges or ascidians on deeper temperate rocky reefs and on kelp or seaweed in shallower subtidal habitats. Found as deep as 33 ft (10 m).

BEHAVIOR
In addition to its cleaning behavior, this species probably is territorial.

FEEDING ECOLOGY AND DIET
A cleanerfish, it feeds upon ectoparasites plucked from various species of fishes.

REPRODUCTIVE BIOLOGY
Poorly known, but females deposit eggs on algae within a male's territory, and both parents provide care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆

Northern clingfish
Gobiesox maeandricus

FAMILY
Gobiesocidae

TAXONOMY
Gobiesox maeandricus Girard, 1858, San Luis Obispo, California, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
There are 13–16 dorsal soft rays; 12–14 anal soft fin rays; a rounded caudal fin; and short, rather broad pectoral fins with a fleshy palp that bridges between the base of the fin and the gill opening. The color pattern consists of a light olive-brown or cherry-red background with either dark reticulations or mottled shades of lighter color and a series of white bars between the eyes. In juveniles the white bars also run along the back and on the edge of the caudal fin. Grows to about 6.3 in (16 cm) in length. Males tend to be larger than females.

DISTRIBUTION
Eastern Pacific from southeastern Alaska south to southern California; also found at Revillagigedo Island off Baja California, Mexico.

HABITAT
Lives among algae or under rocks in the intertidal zone and in the upper canopy of kelp forests, to a depth of 26 ft (8 m). The ability to breathe atmospheric air with its gills allows it to tolerate exposure, if it is kept moist under rocks or algae.

BEHAVIOR
Males maintain territories. Both males and females tend to be somewhat secretive, clinging to surfaces and moving only to feed or interact with others.

FEEDING ECOLOGY AND DIET
Feeds upon small mollusks and crustaceans found on rocks, algae, and kelp.

REPRODUCTIVE BIOLOGY
As with others in this genus, this species likely spawns demersal eggs in a nest prepared by a male within his territory.

Spawning may take several hours. Males provide parental care. The larvae are planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected mainly for public aquaria. ◆

Pygmy shore-eel
Alabes parvulus

FAMILY
Gobiesocidae

TAXONOMY
Alabes parvulus McCulloch, 1909, rock pools near Sydney, New South Wales, Australia.

OTHER COMMON NAMES
None known.

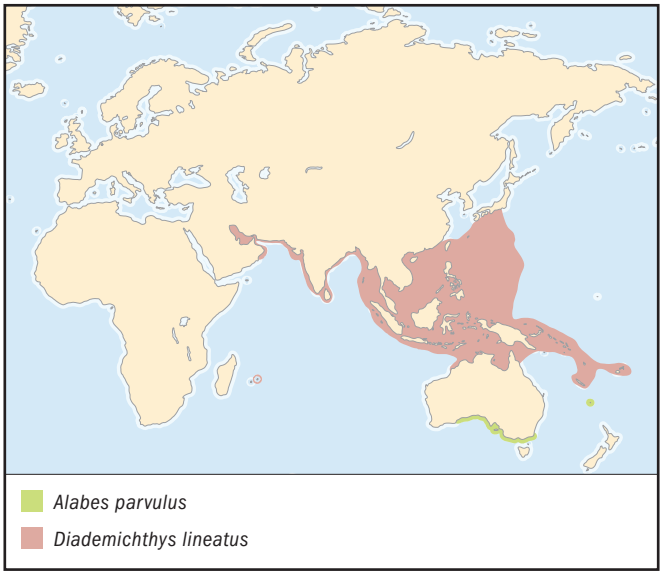
PHYSICAL CHARACTERISTICS
Elongate and eel-like body with reduced fins. Vestigial sucking disc. Grows to 1.9 in (5 cm) in length.

DISTRIBUTION
Temperate waters of southern Australia and Norfolk Island.

HABITAT
Inhabits the intertidal zone. Found in tide pools, in brown seaweed beds and under rocks, to a depth of 20 ft (6 m).

BEHAVIOR
Poorly known. Has been found in small groups of three to six individuals, and social interactions may be expected to take place regularly.

FEEDING ECOLOGY AND DIET
Feeds upon small benthic invertebrates.



REPRODUCTIVE BIOLOGY
Largely unknown. Spawning is probably seasonal, during warmer months, and is paired with the deposition of demersal eggs. Larvae are probably planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆

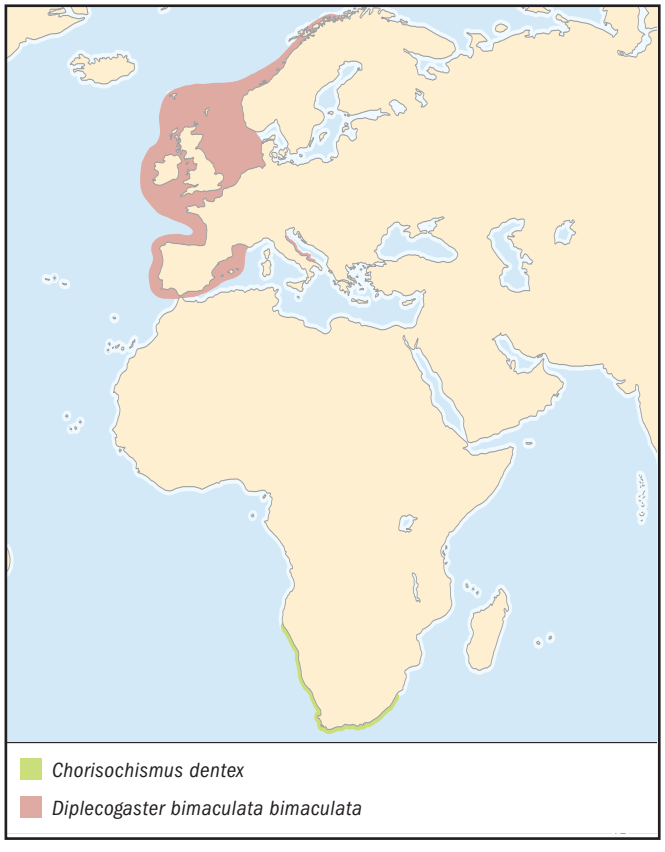
Rocksucker
Chorisochismus dentex

FAMILY
Gobiesocidae

TAXONOMY
Chorisochismus dentex Pallas, 1769, type locality not specified.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Large, tadpole-like body with a very broad head. There are 7–9 dorsal fin soft rays, 6–7 anal fin soft rays, 21–24 pectoral fin soft rays, and 8–10 caudal fin rays. The teeth are large and conical in shape. Perhaps the largest of all clingfishes, this species reaches 11.8 in (30 cm) in length.



DISTRIBUTION
Southeast Atlantic, from Namibia south to northern Natal in South Africa.

HABITAT
Tide pools and rocks and boulders in the intertidal zone.

BEHAVIOR
Poorly known. Males likely are territorial. Owing to its large size, rocksuckers are probably more mobile than other demersal clingfishes.

FEEDING ECOLOGY AND DIET
A carnivore that preys upon limpets and sea urchins. This species uses its large upper incisiform teeth to pry limpets off rocks. The undigested shell fragments are passed through the gut and emerge in mucous capsules.

REPRODUCTIVE BIOLOGY
Poorly known. Females probably lay demersal eggs in a male's territory, and the male performs parental care. The larvae are probably planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆

Sonora clingfish
Tomicodon humeralis

FAMILY
Gobiesocidae

TAXONOMY
Tomicodon humeralis Gilbert, 1890, Puerto Refugio (Angel Island) and La Paz, Mexico.

OTHER COMMON NAMES
Spanish: Chupapiedra de Sonora.

PHYSICAL CHARACTERISTICS
Compressed, elongate body with a broad head and a large sucking disc. There are 8–9 dorsal fin soft rays, 6–7 anal soft fin rays, 17–19 pectoral fin soft rays, and 9–10 caudal fin soft rays. The color pattern consists of light diagonal stripes along the entire body, with a pair of dorsal spots positioned just behind the head, about even with the pectoral fins. Grows to 3.3 in (8.5 cm) in length. Sexually dimorphic, with males larger than females.

DISTRIBUTION
Endemic to the Gulf of California from Punta Borrascoso to Guaymas in Sonora and from San Felipe to Cabo San Lucas in Baja California.

HABITAT
A common clingfish found mainly in the upper and mid-intertidal zones, usually under rocks, to which they cling, and in little or no water. If kept moist, this fish is able to withstand extreme temperatures when exposed to air.

BEHAVIOR
This species is secretive, clinging to the undersides of rocks and moving over rocky surfaces to feed. Their movements are related to tidal movements. Activity is greater at high tide, and there is little or no activity at low tide. Males are territorial. Both males and females secrete large amounts of mucus, which coats their bodies and protects them from desiccation.

FEEDING ECOLOGY AND DIET
A diurnal predator that feeds upon small crustaceans, including barnacles and limpids.

REPRODUCTIVE BIOLOGY
Spawning begins in late spring or early summer and is paired with demersal courtship. A single male may mate with more than one female. Eggs are adhesive and laid on the underside of rocks, where they are guarded by the male, sometimes with the aid of one or more females. During low tide, the parents secrete mucus that protects the eggs from exposure. The larvae are planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be collected infrequently for aquaria. ◆

Two-spotted clingfish
Diplecogaster bimaculata bimaculata

FAMILY
Gobiesocidae

TAXONOMY
Diplecogaster bimaculata bimaculata Bonnaterre, 1788, seas of England, although no types were designated.

OTHER COMMON NAMES
English: Two-spotted sucker.

PHYSICAL CHARACTERISTICS
Flattened and elongated body, with a somewhat triangular snout. The dorsal fin has 4–7 soft rays, and the anal fin has 4–7 soft rays. The gill opening is minute. Color varies but usually is red with yellow on the ventral surface and a pattern of blue and brown spots over the body surface. Males are distinguished by a purple or red spot, ringed in yellow, on each flank, behind the pectoral fins. Grows to 2.4 in (6 cm) in length.

DISTRIBUTION
Eastern Atlantic Ocean, from Norway and the Faroe Islands south to Gibraltar and the western Mediterranean and Adriatic. The subspecies *Diplecogaster bimaculata euxinica* is found in the Black Sea and *D. bimaculata pectoralis* from the offshore Canary and Cape Verde Islands and the Azores.

HABITAT
A temperate species found on sea grass beds, rocky bottoms, bivalve banks, and mud bottoms. Reported to favor shells. Depths range between 59 and 180 ft (18–55 m) in cooler waters and down to 328 ft (100 m) in the warmer Mediterranean.

BEHAVIOR
Not well known. Males likely are territorial.

FEEDING ECOLOGY AND DIET
Feeds on small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Demersal courtship and spawning occur in the spring and summer months, with golden-colored eggs laid in masses under shells or stones. Males provide most of the parental care. Larvae are planktonic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Occasionally recovered from trawls working soft mud bottoms or bivalve banks. ◆

Urchin clingfish
Diademichthys lineatus

FAMILY
Gobiesocidae

TAXONOMY
Diademichthys lineatus Sauvage, 1883, New Caledonia.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Elongate and slender body, with spatulate snout and small fins. There are 13–15 dorsal fin soft rays, 12–14 anal fin soft rays, and 25–26 pectoral fin soft rays. Color is reddish or reddish brown, with paired yellow stripes and a yellow blotch on the caudal peduncle that extends to the caudal fin. Grows to 1.9 in (5 cm) in length.

DISTRIBUTION
From Oman and Mauritius in the western Indian Ocean east to Indonesia and Fiji, north to southern Japan, and south to northern Australia.

HABITAT
Inhabits shallow coral reefs among the long-spined sea urchins and branching corals, usually in holes or protected areas.

BEHAVIOR
This clingfish swims, often in a dancing or undulating motion, between the spines of sea urchins, within coral heads, and in holes or small caves where sea urchins might be found. Their behavior is not known in any great detail and remains to be studied.

FEEDING ECOLOGY AND DIET
Takes burrowing bivalves on corals, eggs of shrimp commensal with sea urchins, and the tube feet of sea urchin hosts. Juveniles feed on the pedicellariae and sphaeridia of host urchins and on copepods and the eggs of shrimp that are commensal with sea urchins.

REPRODUCTIVE BIOLOGY
This species probably courts and spawns in a manner similar to that of others in its family, except that courtship bouts most likely take place in the water column. The eggs are small and demersal, and the larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN. May be at risk from the loss of sea urchins because of overfishing, disease, or other factors and from habitat destruction and the effects of pollution on reefs.

SIGNIFICANCE TO HUMANS
May be collected for the aquarium trade. ◆

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Gosline, W. A. "A Reinterpretation of the Teleostean Fish Order Gobiosociformes." *Proceedings of the California Academy of Sciences* series 4, 37 (1970): 363–382.

Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Terry J. Donaldson, PhD

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Callionymoidei
(Dragonets and relatives)

Class Actinopterygii
Order Perciformes
Suborder Callionymoidei
Number of families 2

Photo: A young fingered dragonet (*Dactylopus dactylopus*) on lava sand near the Sulawesi Island of Indonesia. (Photo by Fred McConnaughey/ Photo Researchers. Reproduced by permission.)

Evolution and systematics

Members of this suborder include the Callionymidae (the dragonets) and the Draconettidae (deepwater dragonets). As with many other perciform fishes, members of this suborder likely radiated in the Eocene period. The systematic placement of this suborder begs further consideration as it has been placed under the nonperciform order Gobiesociformes (Gosline, 1970; Leis and Carson-Ewart, 2000), or linked to the family Gobiesocidae in a closely related suborder, the Gobiesocoidei, within the Perciformes (Helfman et al., 1997).

The Callionymidae consists of at least 17 genera and 156 species, although exact numbers vary because of two different and competing classifications proposed by T. Nakabo (1982 and 1983) and R. Fricke (1983). The Callionymidae genera include:

- *Anaora* (one species)
- *Bathycallionymus* (two subspecies)
- *Callionymus* (82 subspecies)
- *Calliurichthys* (one species)
- *Dactylopus* (one species)
- *Diplogrammus* (six subspecies)
- *Draculo* (five subspecies)
- *Eleutherochir* (one subspecies)
- *Foetorepus* (eight subspecies)
- *Neocynchiropus* (two subspecies)
- *Paracallionymus* (one subspecies)
- *Paradiplogrammus* (two subspecies)
- *Progogrammus* (one species)
- *Pseudocalliurichthys* (three subspecies)
- *Repomucenus* (10 subspecies)
- *Spinicapitichthys* (one species)
- *Synchiropus* (29 subspecies)

The Draconettidae consists of only two genera, *Centrodraco* (10 subspecies, but one with 2 subspecies) and *Draconetta* (one species).

Physical characteristics

The Callionymidae are relatively small, sometimes diminutive, usually elongate fishes, having both a depressed trunk and broad or depressed head. Most of these fishes are sexually dimorphic. Males tend to have larger body sizes and dorsal fins, greater fin ornamentation, and more distinctive color patterns. Dragonets usually have 2 dorsal fins, the first containing 1–4 spines, the second has only 6–11 rays; the last ray is divided at the base, as in the anal fin. Dorsal fins of males may also be large or high, and also have elongated rays. Dragonets also have relatively large pelvic and pectoral fins, with the former positioned forward of the latter. The anal fin has 4–10 rays. The shape of the caudal fin varies, but may be elongate or spade-like and include elongated rays. The preoperculum has well-developed spines and bars along the margin, but no opercular or subopercular spines are present. Dragonets are further distinguished by the presence of small gill openings, generally pore-like, positioned at the top of the head or along the upper flanks, with gill membranes that are united at the isthmus that separates the gills. Their bodies lack scales, but their lateral lines are quite well developed. Many species have color patterns well suited as camouflage, but others are brilliantly, if not spectacularly, colored. Some species, such as members of the genus *Foetorepus*, produce an acidic, bitter-tasting slime that covers their bodies and may serve as a toxic deterrent to predators.

Dragonet larvae develop quite rapidly, and most species are able to settle with a full compliment of fins at a small size. The larvae are denoted mainly by having a relatively large head, a short snout that lengthens with growth, a small, protrusible mouth placed terminally on the head, the presence of teeth only after settlement, a large eye that migrates dorsally with growth, and a gas bladder located anterior to the gut, which disappears in adults. The gills are free from the isthmus at first but become attached after the larvae undergo flexion. The bodies of dragonet larvae are heavily pigmented, with most of the pigment concentrated on the ventral, rather than dorsal, surface of the body.

The Draconettidae have small, elongated, and rounded bodies, pointed snouts, relatively large pectoral fins, and elongated pelvic fins. The gill openings are relatively broad. There are two nostrils on each side of the head. Scales are absent, but the body is distinguished by the presence of a grooved or vestigial lateral line that is well developed on the head. These fishes are also distinguished by having large eyes. There are two dorsal fins, with three spines on the first and 12–15 rays on the second. There are 12–13 soft rays on the anal fin. The operculum and suboperculum have single strong spines but these are absent on the preopercle. Their larvae are very poorly known. The body is elongate and compressed, the head is also compressed and is of moderate size, the snout is pointed, and the mouth is small and reaches as far as the anterior margins of the large, round eyes. The gas bladder is absent, and the fin elements are present in larvae at least 0.31 in (0.8 cm) long.

Distribution

The Callionymidae are found in tropical and warm temperate waters of the Atlantic, Indian, and Pacific Oceans. Species are found at either continental or insular localities, however most species occur in the Indo-Western Pacific. The Draconettidae share approximately the same broad distribution, but are limited to seamounts or deeper edges of continental shelves, and thus live at cooler water temperatures.

Habitat

Most members of the Callionymidae are found on coral pavement, rubble, sand, mud, or on other soft bottoms. Some species occur exclusively in corals, tide pools, or among rocks; however, others may be found among algae-covered rocks on flats or shorelines, or mangrove roots in brackish water. The two species of the genus *Bathycallionymus* occur on deep flats. Members of the family occur within a depth range of less than 39 in (1 m) at low tide to over 1,312 ft (400 m). Little is known about the habitats of the Draconettidae. They may likely be found in rubble and sand or amongst rocks along deep-slope edges or on top of seamounts.

Behavior

The behavior of dragonets has been studied for only a few species and, for these, most effort has been directed toward reproductive behavior. Males utilize their longer first dorsal fins for displaying in both male-male aggressive encounters, and male-to-female social and courtship interactions. Male body color may also be utilized, especially during courtship.

Virtually nothing is known about the behavior of members of the Draconettidae. Their large eyes likely aid them in movement, feeding, social interactions, and reproductive behavior in deep demersal habitats. The dorsal fins of males may be utilized for signaling, but their effectiveness under dimly lit conditions remains to be demonstrated.

Feeding ecology and diet

Callionymids and draconettids feed on small benthic invertebrates. Larger species, such as members of the callionymid genera *Callionymus*, *Foetorepus*, *Repomucenus*, and *Synchiropus*), feed upon correspondingly larger prey. Predators of dragonets and draconets are not well known, but it is likely that they are preyed upon by larger benthic-feeding or opportunistic predatory fishes.

Reproductive biology

Dragonets appear to be gonochoristic, with no evidence of sex change reported. Males maintain relative large home ranges compared to females and these may be defended territorially during periods of reproduction. Mating systems may consist of pairs or single-male dominated mating groups of two or more females. Some smaller, cryptically colored males may also be in these mating groups and will attempt to court and spawn with females, but will often fail because of aggressive interactions with the dominant male. Courtship and spawning typically commences prior to sunset for most species or possibly just after dawn in some species. A male will approach a female and display his erect fins to her, and, as if carrying her, will ascend with her a short distance into the water column, where pelagic eggs are released and fertilized. These eggs are spherical in the genera *Calliurichthys* and *Repomucenus*, and in *Callionymus* from the Atlantic Ocean. The mangrove dragonet (*Paradiplogrammus enneactis*), and perhaps others in this genus, produces a buoyant egg mass that later breaks up prior to hatching. Spawning may be seasonal, depending upon latitude and water temperature, and may demonstrate one or more peaks during an annual cycle. Serial spawning, with the daily production of eggs during the season, has been suggested for some species. Smaller females of some species with bimodal spawning seasons may defer reproduction until the second season (late summer or autumn).

Next to nothing is known about the reproductive biology of the Draconettidae. Both the spawning mode and eggs are unknown. Owing to their close relationship with the Callionymidae, they are sexual dimorphic, with males being larger than females. They are not likely to be hermaphroditic. Spawning is probably paired and pelagic, with a rapid, short ascent into the water column where eggs and sperm are released.

Conservation status

One species of callionymid, the St. Helena dragonet (*Callionymus sanctaehelenae*), which is endemic to the island of St. Helena in the South Atlantic, is currently listed by the IUCN

as Critically Endangered. Some callionymids important to the aquarium trade, such as the mandarinfish (*Synchiropus splendidus*) and *Repomucenus* spp. that are important as food fishes, may also be at risk from overfishing, habitat destruction, and recruitment failure as a consequence of pollution or the creation of anoxic conditions that lead to hypoxia among larvae. No members of the Draconettidae are listed by the IUCN, but these fishes may be at risk from the effects of the deep trawling of their habitats.

Significance to humans

A number of dragonet species are important in the aquarium trade, such as the mandarinfish, and some species, such as *Repomucenus* spp., are taken directly or as bycatch in commercial or subsistence food fisheries, or for the production of fish meal. The Draconettidae may be taken incidentally by deep-trawling fishing vessels, but appear not to have any commercial significance to humans.

1. Draconett (*Centrodraco insolitus*); 2. Draconetta (*Draconetta xenica*); 3. Richardson's dragonet (*Repomucenus richardsonii*); 4. Mandarinfish (*Synchiropus splendidus*); 5. Lancer dragonet (*Paradiplogrammus bairdi*). (Illustration by Marguette Dongvillo)

Species accounts

Lancer dragonet
Paradiplogrammus bairdi

FAMILY
Callionymidae

TAXONOMY
Paradiplogrammus bairdi Jordan, 1888, off Pensacola, Florida, United States.

OTHER COMMON NAMES
English: Coral dragonet; Spanish: Dragoncillo coralino.

PHYSICAL CHARACTERISTICS
Total length 4.5 (11.4 cm). Sexually dimorphic; males are larger, have larger fins, extended dorsal fin, and more distinctive color patterns on body and fins. Body is elongate and scaleless in both sexes. Have 4 dorsal spines on first dorsal fin, 9 soft rays on second dorsal fin; 8 anal fin rays, but no spines. Color pattern is complex and varies between sexes. Dorsal half of body has marbling and mottling in various shades of brown, black, and white; white, roundish blotches between narrow brown bars on ventral half of body. First dorsal fin of male marked by yellow swirl and second dorsal fin with downward-pointing pattern of dark bands. Males also have blue concentric lines and rows of spots on first dorsal fin, blue bars with narrow orange margins on preopercle, orange spots, small blue lines and crescentlike markings on dorsal half of body, and blue spots around ventral half of eyes.

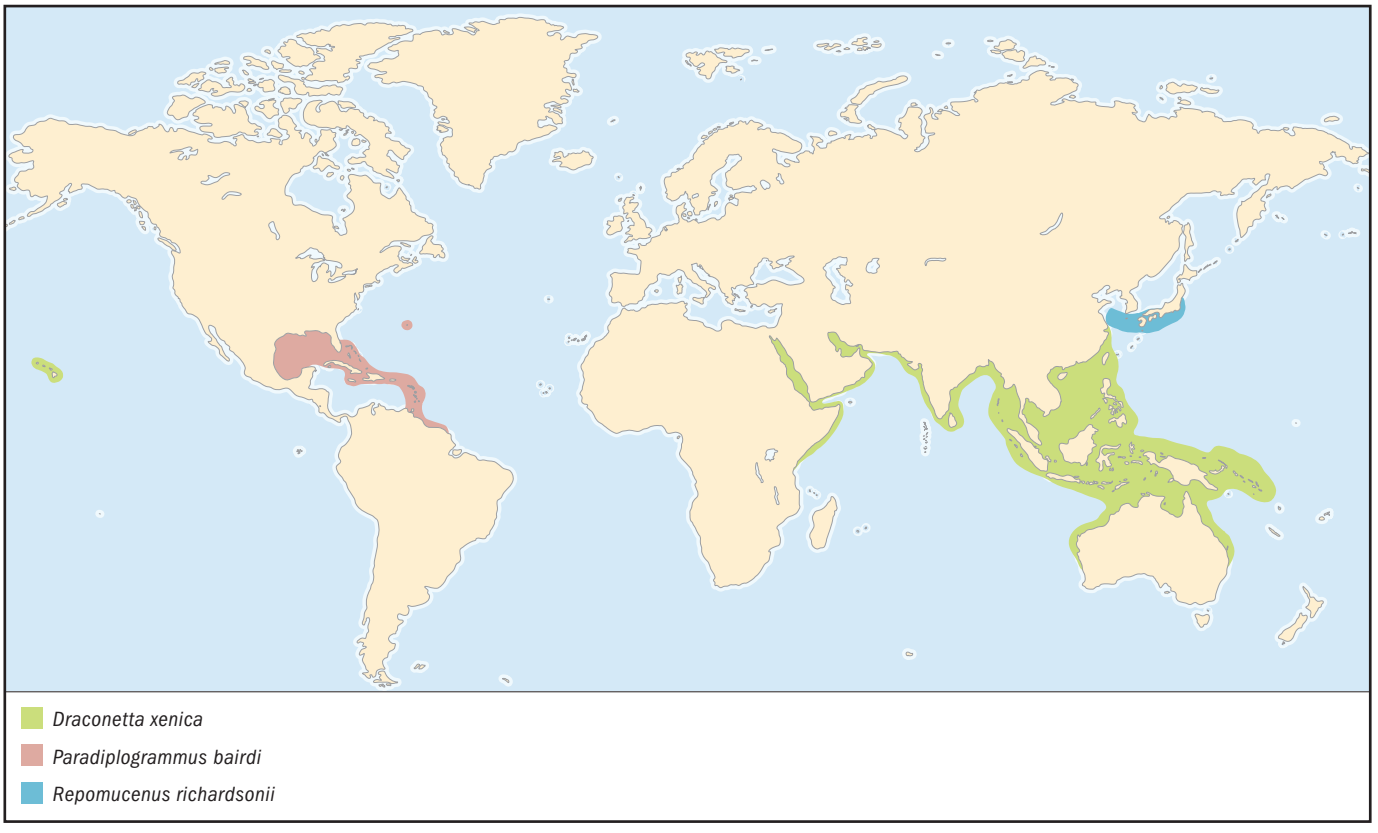
DISTRIBUTION
Western Atlantic, from Bermuda and southern Florida, United States, east and south to the Bahamas, south to the Lesser Antilles and northern South America, and west into the Gulf of Mexico.

HABITAT
Benthic; frequents sand patches on shallow reefs, rocky shorelines, and sea-grass flats at depths of 3.3–298.5 ft (1–91 m).

BEHAVIOR
As with other dragonets, utilizes a relatively cryptic coloration to provide camouflage as it forages along the bottom. Social interactions, especially between males, can include the defense of territories or females, and are distinguished by erect fin displays.

FEEDING ECOLOGY AND DIET
Feeds upon small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Hermaphroditism has not been reported. Sexually dimorphic characters in males, mainly fin size, are used in reproductive behavior. Males initiate courtship by displaying erect fins towards females. Spawning is paired and occurs after short ascent into water column, where the eggs are fertilized. Eggs are pelagic, egg mass is likely buoyant and breaks up prior to hatching. Larvae generally typical of other dragonets.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade. May be taken incidentally in bottom trawls by fishing vessels operating on offshore banks, but of no value as a food fish. ◆

Richardson's dragonet
Repomucenus richardsonii

FAMILY
Callionymidae

TAXONOMY
Repomucenus richardsonii Bleeker, 1854, Nagasaki, Japan.

OTHER COMMON NAMES
Japanese: Nezumi-gochi.

PHYSICAL CHARACTERISTICS
Total length 6.7 (17 cm). Sexually dimorphic in character development. Body elongate and strongly depressed with broad, flattened head. Scales lacking. First dorsal fin with 4 spines; 9–10 soft rays on second, elongated dorsal fin. Anal fin has 9–10 soft rays. Relatively large pectoral and pelvic fins. Caudal fin elongate. Color pattern on body is light to medium brown. Males have three dark blotches on first dorsal fin and oblique dark lines along lower half of flank. Faint dark mottling on anal fin and ventral portion of caudal fin. Females and young males have large black mark on first dorsal fin; females also have three faint white spots on second dorsal fin. May live only as long as two years.

DISTRIBUTION
Northwestern Pacific, from central Japan west into the East China Sea.

HABITAT
Coastal bottoms of sand and mud.

BEHAVIOR
Behavior not well known. Species is suited for movement, foraging, and crypsis on sandy or muddy bottoms. Social interactions include aggressive behavior between rival males, usually during courtship periods, with larger males dominating smaller ones. Aggressive behavior is characterized by display of erect fins during interactions.

FEEDING ECOLOGY AND DIET
Feeds mainly upon benthic invertebrates.

REPRODUCTIVE BIOLOGY
Pronounced sexual dimorphism in color, body size, and fin development; males have greater body size as well as elongated fin spines and rays. These differences contribute toward reproductive success because of their value in defending against rival males or their signal function in attracting females. Courtship and spawning is paired, and commences with male displays of erect fins and results in pelagic spawning in water column. Eggs produced serially, likely spawned on daily basis with one or two spawning seasons (spring and early autumn). No evidence of hermaphroditism. Recruitment of larvae is also seasonal.

CONSERVATION STATUS
Not listed by the IUCN. May be vulnerable or threatened by overfishing, habitat destruction, and pollution that causes anoxic conditions.

SIGNIFICANCE TO HUMANS
Occurs in both subsistence and commercial fisheries. Flesh favored in Japan. Also collected for the aquarium trade. ◆

Mandarinfish
Synchiropus splendidus

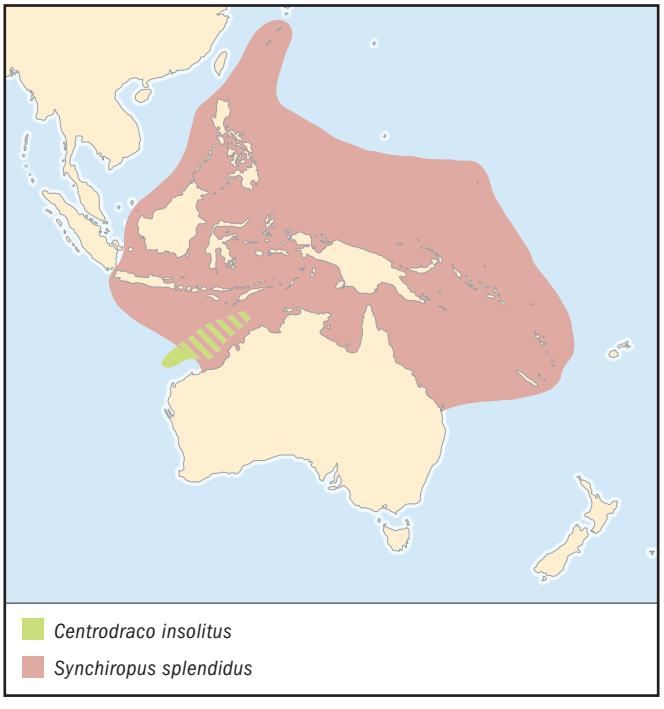
FAMILY
Callionymidae

TAXONOMY
Synchiropus splendidus Herre, 1927, Bungau, Philippines.

OTHER COMMON NAMES
Japanese: Nishiki-teguri.

PHYSICAL CHARACTERISTICS
Total length about 3.1 in (8 cm). Sexually dimorphic; males larger than females and have larger dorsal fins. Small, somewhat elongated body lacks scales but has well-developed lateral line. Two dorsal fins, first with 4 spines and second with 8 dorsal rays. There are 6–8 soft rays on the anal fin. The preopercle has strong spine, but no spines present on operculum or suboperculum. Body coloration of vivid green or blue markings on ground color of orange, or rarely red.

DISTRIBUTION
Western Pacific and eastern Indian Ocean from the Philippines and Indonesia (Java), east to Pohnpei (Micronesia) and New Caledonia, south to northwestern Australia (Rowley Shoals) and to the southern Great Barrier Reef, and north to



the Ryukyu Islands of southern Japan. May also occur in Tonga.

HABITAT
Coral reefs on inshore reefs and in protected lagoons. Microhabitat mainly coral heads, silty rubble, and even leaf litter. Ranges in depth 3.3–59 ft (1–18 m).

BEHAVIOR
Generally solitary and cryptic within a home range. Emerges to feed during early morning, just before dusk, or in cloudy weather. Social interactions are relatively few and usually not aggressive.

FEEDING ECOLOGY AND DIET
Feeds upon small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Gonochoristic and polygynous, with a single male mating with more than one female daily. Courtship and spawning occurs during short period at dusk throughout most of the year. Females move to one or more specific areas before the onset of courtship. Males also move to and between these areas seeking females to court. Larger males dominate smaller males and prevent them from courting with females. Males use elaborate fin displays and circle females repeatedly during courtship. More than one bout of courtship may be necessary before a female is ready to spawn. Then, the pair rises slowly into the water column to spawn and fertilize a small batch (12–205) of pelagic eggs. After spawning, female returns to her home area to sleep, and male moves on to attempt to court and spawn with other females. Reported to have been bred in captivity. Larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN. May be vulnerable or threatened by overfishing, destructive fishing (including the use of cyanide), and destruction of habitat.

SIGNIFICANCE TO HUMANS
Important and highly prized aquarium fish harvested mainly in Southeast Asia and imported to the United States as part of the aquarium trade. ◆

Draconett
Centrodraco insolitus

FAMILY
Draconettidae

TAXONOMY
Centrodraco insolitus McKay, 1971, off northwest Australia (17°17′ S, 119°51′ E, at a depth of 1,148 ft [350 m]).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Total length about 5.1 (13 cm). Small, elongate, rounded body lacking scales. Lateral line grooved. Large eye and pointed snout. Two dorsal fins with three dorsal spines present on the first; the first dorsal spine is the longest. Both operculum and preoperculum have a single strong spine. Last dorsal and anal rays are branched, others are simple. Pectoral fin large and rounded. Pelvic fin elongate. Body pink with yellow blotches, and dark spots near pectoral fin and caudal peduncle.

DISTRIBUTION
Eastern Indian Ocean off coast of northwest Australia.

HABITAT
Deep-bottom rubble and sand to 1,040–1,148 ft (317–350 m) deep.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Likely feeds upon small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Nothing known, but likely a pelagic spawning fish with paired courtship. Sexually dimorphic; males larger than females.

CONSERVATION STATUS
Not listed by the IUCN. May be vulnerable to damage caused by deep trawling of habitats.

SIGNIFICANCE TO HUMANS
No direct significance. May be taken incidentally in deep-trawling fisheries. ◆

Draconetta
Draconetta xenica

FAMILY
Draconettidae

TAXONOMY
Draconetta xenica Jordan and Fowler, 1903, Suruga Bay, Namazu, Japan.

OTHER COMMON NAMES
Japanese: Inaka-numeri.

PHYSICAL CHARACTERISTICS
Standard length 3.5 in (9 cm). Small, elongate, rounded body lacks scales but has grooved lateral line. Eye is large and snout pointed. There are two dorsal fins with three dorsal spines present on the first; first dorsal spine is the longest. Operculum and preoperculum have single strong spine. Last dorsal and anal rays branched, others are simple. Pectoral fins large and rounded, pelvic fins elongate. Body pink to whitish pink, with pink markings on dorsal, anal, and caudal fins.

DISTRIBUTION
Continental edges from East Africa to the Hawaiian Islands.

HABITAT
Deep-bottom rubble or sand.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Probably feeds upon small benthic invertebrates.

REPRODUCTIVE BIOLOGY
Largely unknown, but likely a pelagic spawning fish with paired courtship. Sexually dimorphic, males larger than females.

CONSERVATION STATUS
Not listed by the IUCN. May be vulnerable to damage caused by deep-trawling of habitats.

SIGNIFICANCE TO HUMANS
No direct significance. May be taken incidentally in deep-trawling fisheries. ◆

Resources

Books

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Terry J. Donaldson, PhD

Gobioidei
(Gobies)

Class Actinopterygii
Order Perciformes
Suborder Gobioidei
Number of families 2–9

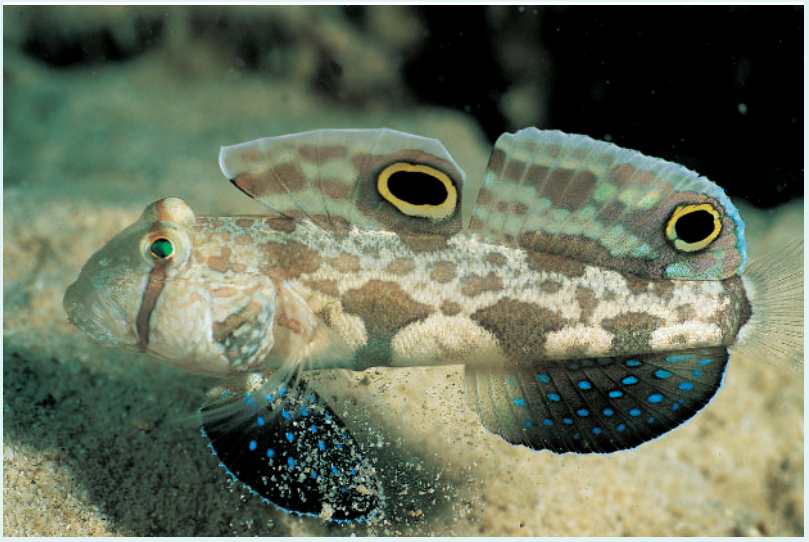


Photo: The twinspot goby (*Signigobius biocellatus*) has false eyespots on its dorsal fin that provide protective mimicry to help ward off predators. (Photo by David Hall/Photo Researchers. Reproduced by permission.)

Evolution and systematics

The suborder Gobioidei contains about 2,121 species in about 268 genera, representing about 9% of living teleostean species. Several different groups of acanthomorphs (spiny-rayed teleosts) have been suggested as the group to which gobioids are most closely related, but the proposed relationships are usually based on relatively little evidence. A morphological study in 1993 suggested that gobioid fishes might be related to one of the following: the gobiesocids (clingfishes) with the callionymoids (dragonets); the trachionoids (weeverfishes and their relatives); or the hoplichthyids (ghost flatheads).

The taxonomy and phylogenetic (evolutionary) relationships within the Gobioidei are also poorly known. It is unsurprising, therefore, that the classification of gobioid fishes has been described as "chaotic." Since 1973 they have been classified in as few as two families, Rhyacichthyidae and Gobiidae; or as many as nine families: Rhyacichthyidae, Odontobutidae, Eleotridae (called Eleotrididae by some authors), Xenisthmidae, Microdesmidae, Ptereleotridae, Kraemeriidae, Schindleriidae, and Gobiidae (including the subfamilies Gobiinae, Amblyopinae, Oxudercinae, Sicydiinae, and Gobionellinae).

Gobioid fishes are characterized by a lack of several bones in the head and axial skeleton, the presence of free sensory neuromasts borne on raised papillae on the head, and sperm-duct glands associated with the testes. The Rhyacichthyidae, or loach gobies, comprising just two species, is accepted as the most primitive gobioid group. The remaining gobioid groups share several features not seen in the Rhyacichthyidae; for example, the modification of the bones in the head, the reduction of the lateral line canal on parts of the head, and the complete loss of the lateral line canal on the body.

Several features of the skeleton and scales unite the seven families of higher gobioids (Eleotridae, Xenisthmidae, Microdesmidae, Ptereleotridae, Kraemeriidae, Schindleriidae, and Gobiidae) into one large group. Some authors apply the name Gobiidae to this whole group, which does not include the Odontobutidae. However, molecular analyses of the cytochrome b genes in gobioid fishes (made in 2000), and morphological analyses (made in 2002) indicate that the Odontobutidae, as distinct from the other higher gobioids, is an artificial assemblage (i.e., the characters that apparently unite species in the Odontobutidae are not genuinely comparable across all the species, or the characters are not restricted only to those species but may also be found in other, unrelated species).

Since 1998 two new gobioid genera, *Protogobius* and *Terateleotris*, have been described with lateral line canals extending onto the body (a primitive feature that is otherwise restricted to the Rhyacichthyidae). The affinities of these two genera to other gobioid fishes are problematic, and neither has been formally assigned to a family. Morphological evidence suggests similarities between *Protogobius* and *Rhyacichthys*, but this is based mainly on shared primitive features. Analysis of mitochondrial cytochrome b genes also showed that *Protogobius* and *Rhyacichthys* appear to be closely related. *Terateleotris* lacks several of the derived features that are shared by the seven families of higher gobioids, so this group may be related to either of the more basal groups, Rhycichthyidae or Odontobutidae.

A late Cretaceous or early Tertiary origin of gobioid groups has been proposed. Fossil otoliths that might have come from gobioid fishes have been found in the Harudi Formation of Katchchh, India (Lutetian age; 43.6–52 million years old) and the Naggulan Formation of Java (Bartonian

Neon gobies (*Gobiosoma oceanops*) on star coral (*Montastrea annularis*) in Glover's Reef, Belize. (Photo by John Lidington/Photo Researchers, Inc. Reproduced by permission.)

age; 40–43.6 million years ago). The oldest reliably identified skeletal remains are of *Pomatoschistus* (?) cf. *bleicheri* (family Gobiidae), from the Headon Hill Formation, Isle of Wight, Great Britain, and date to the Priabonian age (36.6–40 million years old). The oldest fossil material of any eleotrid gobies are otoliths from Faluns de Gaas, Landes, France, and date to the Rupelian age (30–36.6 million years old).

Gobioids play a particularly important role in the freshwater fish communities of oceanic islands, as well as long-isolated fragments of Gondwana such as Madagascar and Australia.

Physical characteristics

Gobioids are small to medium size fishes, with a cylindrical or laterally compressed body. Most species are between about 1.6 and 3.9 in (40–100 mm) in size but several species are smaller. Approximately 40% of gobioid genera include species under 1.6 in (40 mm) maximum body length, and 22% include species under 1.2 in (30 mm). *Trimmatom nanus* (family Gobiidae) is the shortest known vertebrate at sexual maturity, with females ripening at 0.3 in (8 mm). *Schindleria praematura* (family Schindleriidae) is the lightest known vertebrate at sexual maturity, not weighing more than 0.03 oz (0.8 g). There are some examples of large gobioid fishes, although these are rare and they are usually freshwater species. For example, the fat sleeper (*Dormitator maculatus*) and the marble sleeper goby (*Oxyeleotris marmorata*) in the family Eleotridae are reported to reach over 23.6 in (60 cm) total length.

The gobioid head is usually short and broad, and may be depressed (flattened dorsally). The eyes are positioned on the dorsolateral part of the head. There are usually two separate dorsal fins, the first with five or more weak spines (typically six), and the second dorsal fin with one weak spine and five or more soft, segmented rays. The anal fin also usually has one weak spine and five or more soft, segmented rays. The pectoral fins are generally broad and rounded, but may appear pointed in some species. The paired pelvic fins are positioned thorasically, just below the pectoral fins. Each pelvic fin has one spine and five, soft, segmented rays. The caudal fin is usually broad and rounded, but may appear long and lanceolate in some species. Most species have scales covering the body, although some species lack scales or have them restricted to the posterior part of the body. The size of the scales varies between species, from small and sometimes well embedded in the skin to relatively large. Coloration is variable between species; some are very brightly colored, whereas many others are shades of brown or off white. Both sexes possess a well-differentiated urogenital papilla, posterior to the anus. The urogenital papilla is short and rounded in mature female fish, whereas it is longer and more pointed in mature males.

Gobioid fishes have free, sensory neuromast organs that are distributed on the head in rows of raised papillae. The rows are arranged in diagnostic patterns that are variations of two basic types; a longitudinal arrangement (where all the rows on the cheek run horizontally along the cheek); and a transverse arrangement (where several of the rows run vertically down the cheek). Precise similarities in the arrangement of the papillae rows have been used to infer phylogenetic relationships between groups and hence to classify species. Many gobioid fishes have the pelvic fins united to form a cup-shaped, weakly suctorial disc; this is typical of most, but not all of the Gobiidae, and some of the Microdesmidae and Kraemeriidae. The pelvic fins are separate in the Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotrididae, and Ptereleotridae, and are absent in Schindleriidae.

Distribution

Gobioid fishes are common in the tropics, but may also be found in subtropical and temperate regions. They are absent from polar regions. Most of the species are found in marine coastal waters and in estuaries. They are usually in shallow waters, although some species have been found at depths of about 2,625 ft (800 m). About one-tenth of the known species inhabit fresh waters, including the Orinoco and Amazon River basins in South America, and the Nile, Niger, and Congo River basins in Africa. Some species have very widespread distributions. For example, the dusky sleeper (*Eleotris fusca*) is found in fresh, brackish, and marine waters of the Indo-Pacific, from East Africa through to French Polynesia in the South Pacific. In contrast, some other species have very restricted distributions.

Habitat

Gobioid fishes are found in several diverse marine and brackish-water habitats. About half the known species of gobioid fishes are found in coral reef habitats. Gobiid genera such as *Gobiodon* and *Tenacigobius* spend much of their life among the branches of corals such as the black or thorny corals (Antipatharia) and the sea fans and sea whips (Gorgonacea). Gobiosomine gobies (family Gobiidae) such as *Evermannichthys*, *Risor*, and *Gobiosoma*, include tiny species that live exclusively within sponges.

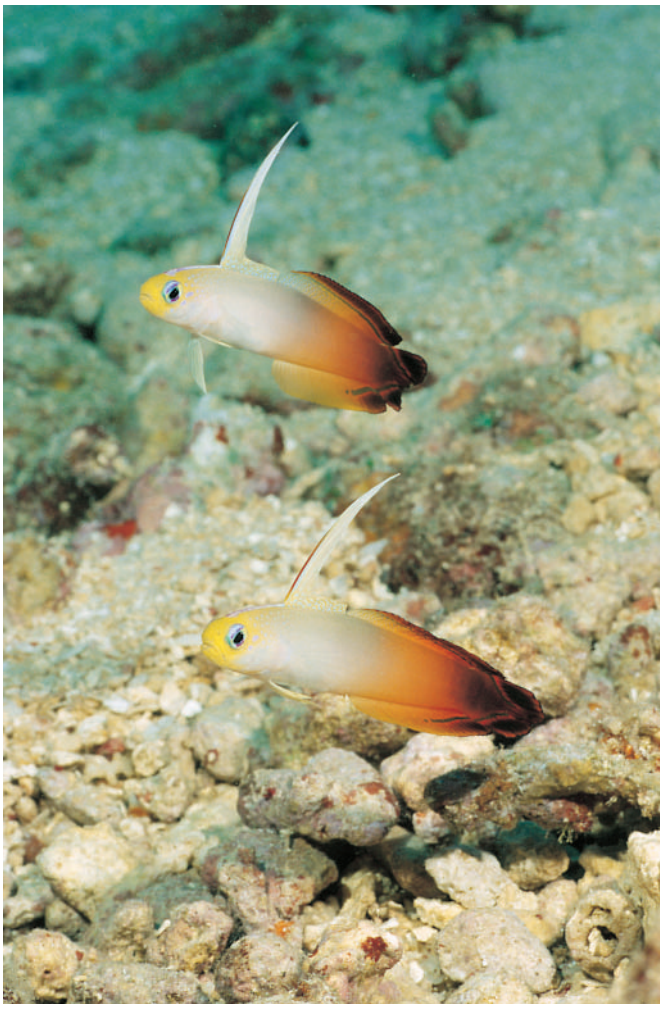
Many gobiid species live epibenthically (on the surface) over sandy or muddy substrates. European species of *Gobius* and *Pomatoschistus* are very common in these habitats. Mudskippers (for example, some species of the gobiid genus *Periophthalmus*) are benthic inhabitants of mangroves. They are highly amphibious, crawling out onto the mud or onto the mangrove roots, and some species also construct burrows, into which they retreat at high tide. Representatives of several other groups of gobioid fishes exhibit a burrowing lifestyle. For example, species of Kraemeriidae (or sand gobies) and the eleotrid genus *Calumia* burrow in sand; the gobiid *Luciogobius* burrows in gravel, and species of amblyopine gobiids burrow in mud. Some species, such as the blind goby (*Typhlogobius californiensis*), from the Eastern Pacific, and the arrow goby (*Clevelandia ios*), live inside the burrows of marine invertebrates.

There are a few examples of blind eleotrid and gobiid species that live in the subterranean fresh waters of caves and sinkholes; for example, *Oxyeleotris caeca* from Papua New Guinea, *Glossogobius ankaranensis* from Madagascar, and the blind cave gudgeon (*Milyeringa veritas*) from Australia. The two species of loach goby (*Rhyacichthys aspro* and *Rhyacichthys guilberti*) show several anatomical specializations for life in torrential rivers and streams. Although the Rhyacichthyidae represents the most basal gobioid lineage, this is not taken as evidence that ancestral gobies also lived in fast-flowing rivers. Instead, it is assumed that this habitat is a specialization of the Rhyacichthyidae. Many species of the Sicydiinae (a subfamily of Gobiidae), including o'opo alamo'o (*Lentipes concolor*), also inhabit torrential hill streams. Their pelvic fins form a strong suctorial disc that allows them to attach firmly to rocks, preventing the fish from being swept away by the swift currents. Some gobies, such as species of *Chlamydogobius*, live in freshwater desert habitats. The Dalhousie goby (*Chlamydogobius gloveri*) can tolerate temperatures up to 111°F (43.9°C); the desert goby (*Chlamydogobius eremius*) can tolerate temperatures between 41 and 106°F (5–41°C), salinities in the range 0–60 parts per thousands and oxygen levels as low as 0.8 parts per million.

Some gobiid species are nektonic, living in the midwater region of shallow coastal waters and estuaries. Cool-temperate midwater dwellers include small aphyiine gobies (family Gobiidae) such as the transparent goby (*Aphia minuta*) and the crystal goby (*Crystallogobius linearis*). Some small nektonic species are also found in warm-temperate and tropical regions; for example, species of *Parioglossus* are found around mangrove roots.

Behavior

Some nektonic species form schools. For example, species of *Parioglossus* or *Gobiopterus* may form small schools around mangrove roots. Epibenthic species are less likely to form schools; however, large populations (in terms of number of individuals) of epibenthic species may be found in some ecosystems. For example, the common goby is densely distributed through some English estuaries. Some species, such as sicydiines, have a larval phase that migrates upriver in schools of very large numbers. The adults of many species are territorial, especially during the breeding season. Some species live in a commensal relationship with invertebrate species. For example, the gorgeous prawn goby (*Amblyeleotris wheeleri*) lives in the burrows of alpheid shrimps. Other species, such as the neon goby, act as "cleaner" fish, picking parasites off large fishes. Mudskippers (e.g., *Periophthalmus barbarus*) are best known for their amphibious lifestyle.



A pair of fire gobies (*Nemateleotris magnifica*) swim over sand and rubble near the islands of Vanuatu Republic. (Photo by Fred McConnaughey/Photo Researchers. Reproduced by permission.)

Feeding ecology and diet

Gobioid fishes commonly feed on invertebrates. Epibenthic species feed on crustaceans, small worms, and insect larvae associated with the benthos. Some coral-dwelling gobies, such as gobiodontines, feed on the polyps of the corals on which they live. Nektonic species living in the water column, such as the glass goby (*Gobiopterus chuno*) from fresh and brackish waters of Asia, feed on plankton. Large eleotrid gobies may feed on other, smaller fish. Various gobioid fish species are specialized for grazing on algae. Sicydiine gobies, such as oopo alamoo have rows of fine teeth that are ideal for scraping algae off rock surfaces. Some algal feeders have

Fighting blue-spotted mudskippers (*Boleophthalmus boddarti*) on a mudflat in Pulau Ubin, Singapore. (Photo ©Tony Wu/www.silent-symphony.com. Reproduced by permission.)

elongate, elaborately coiled guts to assist in the digestion of the tough algal material, e.g., species of *Chlamydogobius* from Australia and *Kelloggella* from the Western Pacific. "Cleaner" gobies, such as the seven-spine, gobiosomine gobies (e.g., *Gobiosoma genie* and the neon goby *Elacatinus oceanops*) are specialized feeders that pick parasites off the scales and skin of other fish, sometimes entering the mouth and gills to extract food items. Another seven-spine goby, the nineline goby (*Ginsburgellus novemlineatus*) shelters on rocks beneath the test, or outer skeleton, of the sea urchin (*Echinometra locunter*) and feeds on the tube feet of the urchin.

The small size of many gobioid species allows them to exploit meiobenthic food resources that are too small for other species. The small size of the gobies might also put them below the threshold for attack by some large, predatory fishes. However, the small size also places the fish at risk from a variety of other predators. For example, coral-dwelling gobiid species of *Eviota* less than 1.2 in (30 mm) long may be eaten by slightly larger coral-dwelling cardinalfishes 1.8–2.1 in (45–53 mm) long. The nineline goby, which hides under sea urchins, can fall prey to long-snouted predators like trumpetfishes, that can delve between the spines of the urchin. Large invertebrates, such as shrimps, can overpower small fishes, and there is a reported case of a small goby being ingested by the nemertean worm *Lineus longissimus*. Small reef-dwelling gobies regularly fall prey to piscivorous mollusks of the genus *Conus*. Freshwater gobioids are regularly preyed upon by water snakes and fish-eating birds.

Reproductive biology

The male may defend a small territory and nest site that, frequently, is a small space under some stones. Often the male is responsible for caring for the developing eggs. The female will lay a few to several hundred small eggs, attaching them to the underside of rocks, vegetation, or onto corals. The eggs usually hatch in a few days, and the young may be dispersed by water currents. In freshwater species such as sicydiine gobies (e.g., o'opo alamo'o), the larvae are probably swept downstream by the water current; they spend a few weeks to months at sea before returning to fresh water. Frequency of spawning is very variable between different species of gobies. Some species, such as the Japanese ice goby (*Leucopsarion petersi*), are typically semelparous species, spawning once in a single spawning season, before dying. Other species are iteroparous, relying on more than one spawning event during their lifespan to achieve a satisfactory reproductive output. This "repeat-spawning" behavior is often seen in small species that face reasonably high predation and a short lifespan. The common goby (*Pomatoschistus microps*), which grows up to 3.5 in (9 cm) total length and can convert 40% of its food into gonad energy, may spawn up to six times over a three-month

period, or as many as nine times during its 18-month life cycle. In contrast, the burrowing species Fries' goby (*Lesuerigobius friesii*) reaches only 1.6 in (4 cm) longer than *P. microps*, but it does not mature until it is two years old, spawns just twice per season, and may live for 11 years. Egg size and number can also vary widely between species of gobies. The smallest eggs are 0.01 in (0.26 mm) in diameter, produced by the empire gudgeon (*Hypseleotris compressa*) from Australia and New Guinea; the largest are 0.1 in (2.4 mm) in diameter produced by the knout goby (*Mesogobius batrachocephalus*) from the Black and Caspian Seas. Some small gobies that live in or around corals and sponges may change sex, which ensures that there are always enough individuals of both sexes to ensure reproduction and survival of the population.

Conservation status

The 2002 IUCN Red List of Threatened Species includes five gobioid species ranked as Critically Endangered and 26 ranked as Vulnerable. Another 21 species are ranked under Lower Risk/Conservation Dependent or Lower Risk/Near Threatened, and 27 are listed as Data Deficient (i.e., there is inadequate information to make a direct, or indirect, assessment of the risk of extinction).

The critically endangered species are threatened by the degradation of their habitat and the introduction of invasive species. For example, *Chlamydogobius micropterus* is from small springs, bores, and drains in Queensland, Australia, that are threatened by water extraction. The Edgbaston goby (*Chlamydogobius squamigenus*) is from similar Queensland habitats that are being degraded by trampling from humans and domestic livestock. The introduction of the mosquitofish (*Gambusia holbrooki*) presents another threat to *C. squamigenus.* The poso bungu (*Weberogobious amadi*), which is restricted to Lake Poso in Sulawesi, was probably last observed in 1985 and might be extinct. It has been threatened by pollution, the introduction of alien fish species to the lake and by diseases carried by those introduced species. The sinarapan (*Mistichthys luzonensis*) from the Philippines was previously thought to be possibly extinct because of the introduction of tilapia to Philippine fresh waters. However, it is still found in lakes of Luzon and is ranked as Lower Risk/Conservation Dependent by the IUCN.

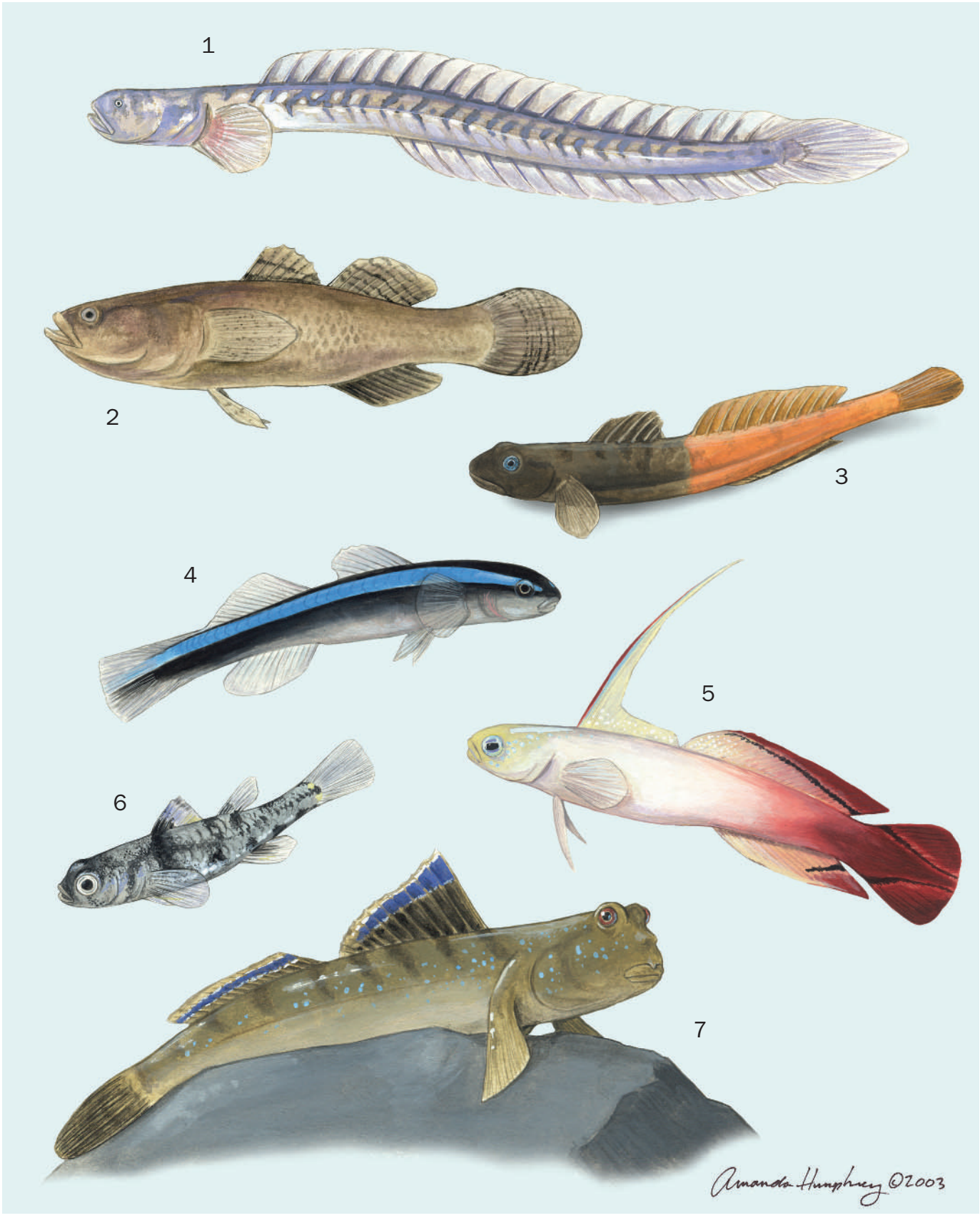
The 26 species listed as Vulnerable include several that have restricted ranges. For example, four of the eight eleotrid species listed as Vulnerable are species of *Mogurnda* that are restricted to a single lake (Lake Kutubu) in Papua New Guinea. The gobiid *Economidichthys trichonis*, which is endemic to Lake Trichonis in Greece, is threatened by agricultural activities that may cause eutrophication of the lake. *Knipowitschia punctatissima* from Italy is threatened by industrial and agricultural activity, and *Knipowitschia thessala* from Greece is threatened because some of its native watercourses are now dry.

Significance to humans

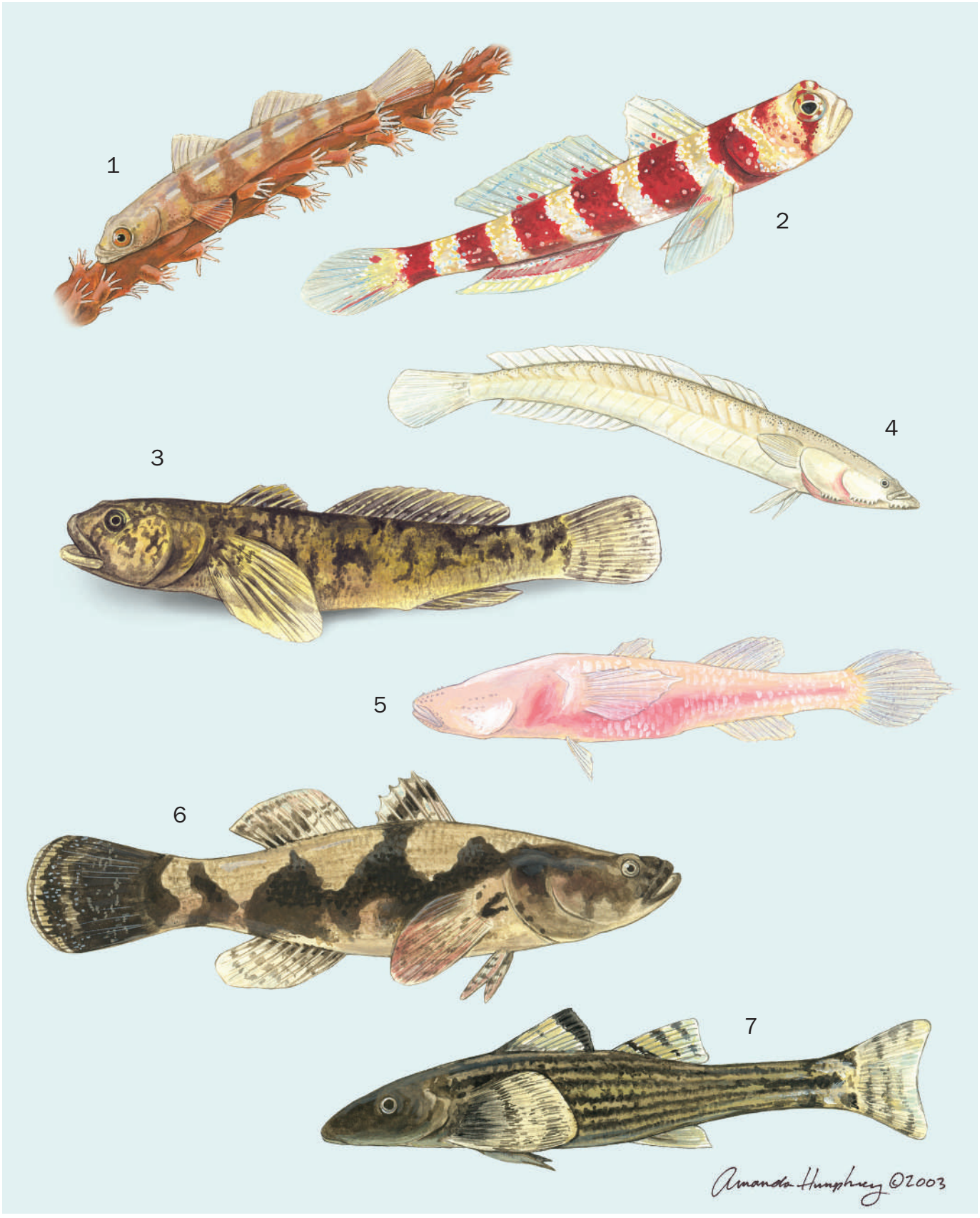
Gobioid fishes do not support important commercial fisheries, but subsistence fisheries exist for some species in the tropical Atlantic and Indo-Pacific. The sinarapan is a delicacy around the Philippine lakes where it is found, and fry of sicydiine gobies are a delicacy in parts of the Caribbean and Indo-Pacific, where they may be made into a paste. According to FAO statistics, the 2000 global capture for all gobioid fishes was 51,199 tons (52,021 tonnes); 63% of this was caught in the northwest Pacific by countries of the Russian Federation, and 15% was caught in the western Central Pacific by the Philippines. Aquaculture produced 376 tons (382 tonnes) of gobioid fishes in 2000, with a value of $3.38 million. Many gobioid species probably represent important food resources to larger fish species that are commercially fished.

Gobioid fishes form a small part of the ornamental fish trade which, by 1992, had a global retail trade value of $3,000 million. In Hong Kong, a major distributor of ornamental fishes, gobies represented only about 1% of the total number of fishes observed in a market survey in 1996 and 1997. Gobies are an important complement of the biological diversity of coral reefs, which are popular sites for tourism. Therefore, these reef-dwelling gobies represent an indirect source of sustainable income to tropical countries that are using their reefs as attractions for properly managed ecotourism.

Introduced species of gobies include the round goby (*Neogobius melanostomus*) in the Great Lakes region of North America; the Japanese goby (*Tridentiger trigonocephalus*), introduced to North American and Australian coastal waters; and the Indo-Pacific *Butis koilomatodon*, introduced into coastal waters of Nigeria, Panama, and Brazil. Translocated *Glossogobius giuris* and *Hypseleotris agilis* appear to have played a role in the extirpation of the endemic cyprinid species flock of Lake Lanao in the Philippines. Native fish species may suffer from competition with these alien species, and the economic cost of monitoring the spread of exotics, and attempting to control them, may be significant.



1. Violet goby (*Gobioides broussoneti*); 2. Large-scale spinycheek sleeper (*Eleotris amblyopsis*); 3. O'opo alamo'o (*Lentipes concolor*); 4. Neon goby (*Gobiosoma oceanops*); 5. Fire goby (*Nemateleotris magnifica*); 6. Dwarf pygmy goby (*Pandaka pygmaea*); 7. Atlantic mudskipper (*Periophthalmus barbarus*). (Illustration by Amanda Humphrey)



1. Whip coral goby (*Bryaninops yongei*); 2. Gorgeous prawn-goby (*Amblyeleotris wheeleri*); 3. Arno goby (*Padogobius nigricans*); 4. Samoan sand dart (*Kraemeria samoensis*); 5. Blind cave gudgeon (*Milyeringa veritas*); 6. Marble sleeper (*Oxyeleotris marmorata*); 7. Loach goby (*Rhyacichthys aspro*). (Illustration by Amanda Humphrey)

Species accounts

Large-scale spinycheek sleeper
Eleotris amblyopsis

FAMILY
Eleotridae

TAXONOMY
Culius amblyopsis Cope, 1871, Suriname.

OTHER COMMON NAMES
English: Sleeper.

PHYSICAL CHARACTERISTICS
Reaches about 3.9 in (10 cm) total length over most of range, largest individual observed from North America about 5.5 in (14 cm). Two dorsal fins, pelvic fins separated, and rounded caudal fin. Torpedo-like body shape with flattened head. Tan to dark brown, sometimes changes to dark trunk laterally with light tan dorsum, especially in juveniles. May have rows of small dark spots on sides. Two dark streaks radiating rearward from eyes on cheeks. A large dark spot on the upper pectoral fin base and some specimens with two elongate spots extending from pectoral fin base onto pectoral fin rays. Stout spine on lower cheek faces forward.

DISTRIBUTION
Common from North Carolina to French Guiana, and in Cuba and Hispaniola. Less frequently known from Brazil and the Antilles.

HABITAT
Euryhaline (able to live in waters of a wide range of salinities); adults and juveniles inhabit continental estuaries, but are also known from fresh water in Central America and occasionally in the Antilles. Associates with floating, emergent, and marginal vegetation, such as mangroves, river cane, and water hyacinths. Pelagic marine larval stage.

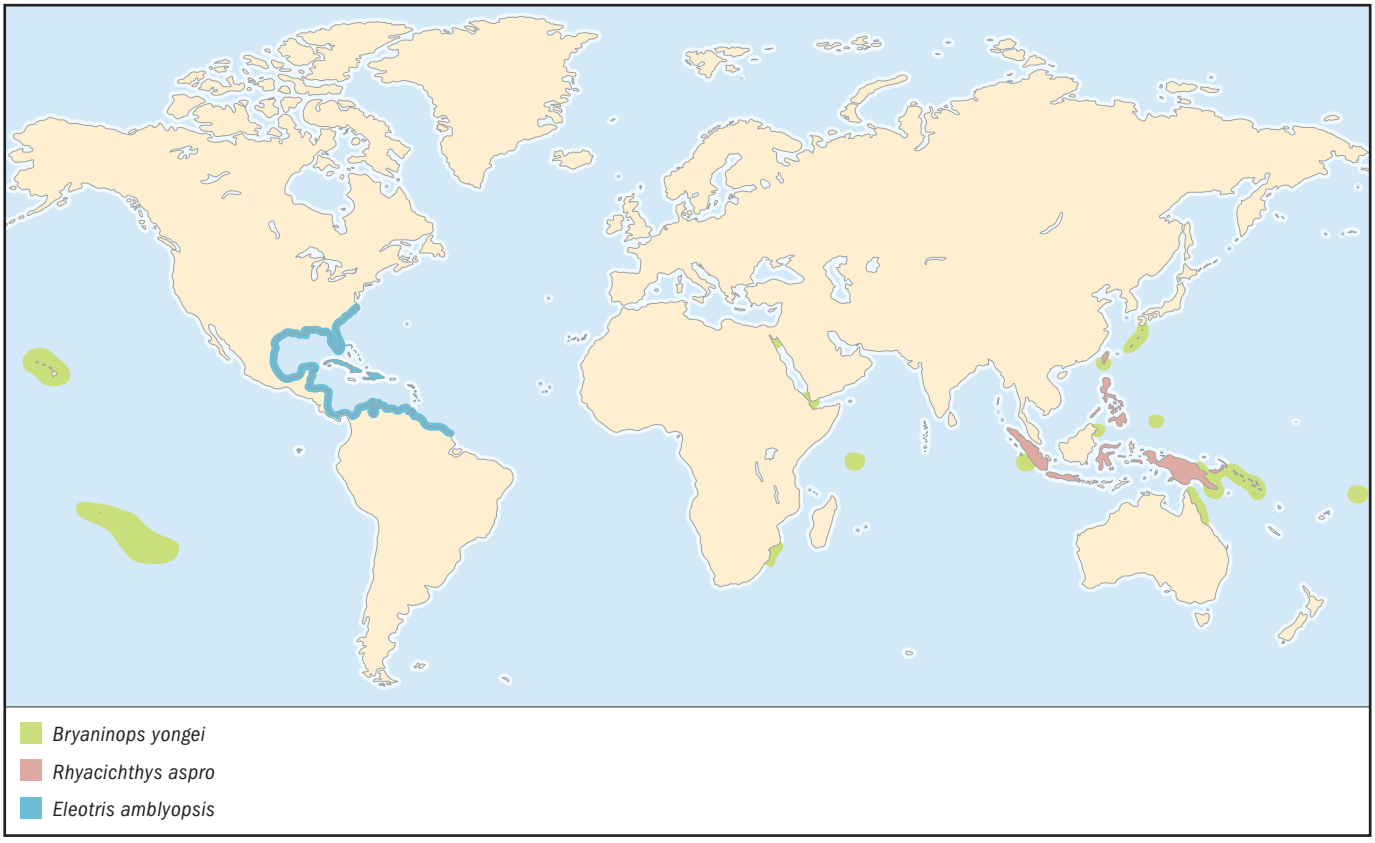
BEHAVIOR
A lethargic "sit-and-wait" predator. Postlarvae join other species to form large schools which periodically move into estuaries and fresh waters after a marine larval period.

FEEDING ECOLOGY AND DIET
Predaceous; feeds on shrimps and small fishes.

REPRODUCTIVE BIOLOGY
Presumably amphidromous, with adults living and reproducing in fresh water or estuaries and a marine larval period.

CONSERVATION STATUS
Considered vulnerable in North Carolina at the edge of its range, but not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



Blind cave gudgeon
Milyeringa veritas

FAMILY
Eleotridae

TAXONOMY
Milyeringa veritas Whitley, 1945, Milyering, Yardie, 20 mi (32 km) southwest of Vlamingh Head, North-West Cape, Western Australia. Populations show a low degree of heterozygosity, which is typical of cave-dwelling fishes. This species is possibly closely related to the Indo-Pacific eleotrid genus *Butis*.

OTHER COMMON NAMES
English: Cave gudgeon.

PHYSICAL CHARACTERISTICS
Reaches about 2 in (5 cm) total length. The head is broad and concave over the snout. The eyes are not visible. Small first dorsal fin with four very short spines. Second dorsal fin with nine longer rays. Pelvic fins separate. The caudal fin is slightly pointed. The head is naked but the body is covered with small scales (about 28 in series along the flanks). The fish is very poorly pigmented. The top of the head is pale yellow, with a dark gray triangular mark over the brain. The posterior nostrils are pink. There is a purplish spot over the operculum. The body is pale gray and fins are flesh colored.

DISTRIBUTION
Western and northeastern coastal plains of the Cape Range Peninsula and Barrow Island, Western Australia.

HABITAT
This is a troglobitic species; i.e., an obligatory cave dweller, found in shallow wells (at depths of up to 1.6 ft/0.5m), sinkholes, and deeper cave systems (at depths of up to 105 ft/32 m) that are freshwater or anchialine (located near the sea and flooded with sea water). In anchialine systems the fishes may live in freshwater layers that overlie the salt water. They are also found in brackish water, tolerating salinities from 0.27–34 parts per thousand and temperatures of 70–83°F (21–28°C).

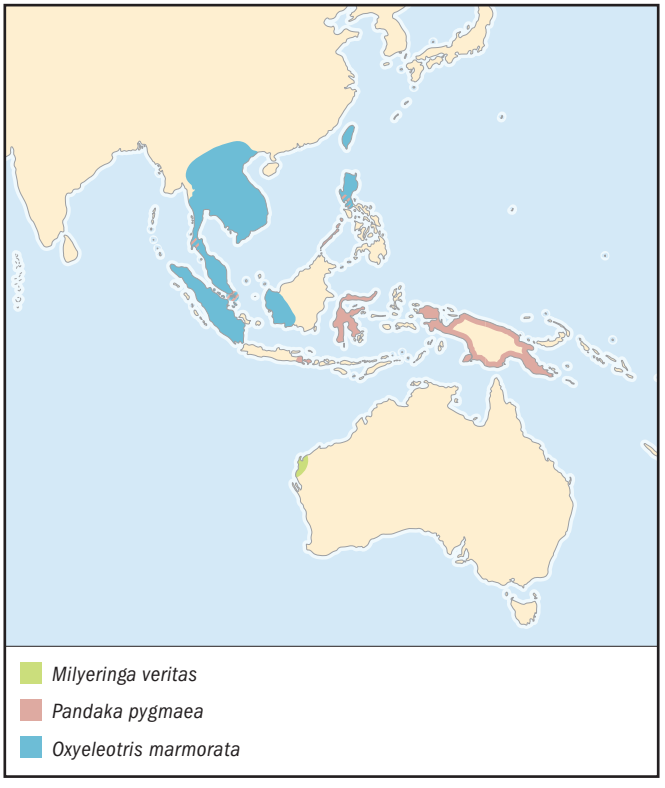
BEHAVIOR
Swims slowly, with the pectorals pointed out to the sides and the pelvics extended slightly forward.

FEEDING ECOLOGY AND DIET
Possibly feeds on insects or other small animals that drop into the cave waters.

REPRODUCTIVE BIOLOGY
Random mating apparently occurs between subpopulations throughout the range.

CONSERVATION STATUS
Listed as Data Deficient in the IUCN 2002 Red List, but as threatened by the Western Australian Conservation Act. Major threats come from habitat disturbance due to urban and agricultural development, and water extraction causing a lowering of the water table. Water quality in the underground systems is being compromised by pollution from nutrients and other chemicals.

SIGNIFICANCE TO HUMANS
None known. ◆



Marble sleeper
Oxyeleotris marmorata

FAMILY
Eleotridae

TAXONOMY
Eleotris marmorata Bleeker, 1852, Bandjarmasin, Borneo, and Palembang, southeast Sumatra, Indonesia.

OTHER COMMON NAMES
English: Marble goby, marbled sand goby; German: Marmorgrundel; Cantonese: Soon hock; Japanese: Kawaanago; Khmer: Trey damrei; Laotian: Pa bou; Malay: Bakutut, belantuk; Tagalog: Bia; Thai: Pla bu jak; Vietnamese: Cá bong.

PHYSICAL CHARACTERISTICS
The largest gobioid fish, this species may reach 35.4 in (90 cm) total length. Torpedo-like body shape with flattened head. Oblique, terminal mouth. Two dorsal fins and rounded caudal fin. Pelvic fins separate. Body brown with dark mottling giving a marbled appearance.

DISTRIBUTION
Southeast Asia in Laos, Cambodia, Vietnam, Thailand, Malay Peninsula, Sumatra and western Borneo. Also reported from Luzon (Philippines), and introduced into Taiwan for aquaculture.

HABITAT
Found in rivers, lakes, swamps, ditches, and ponds; water may be muddy or clear and over muddy, sandy, or gravel bottoms. This species may also be found in brackish waters around the mouths of rivers and canals.

BEHAVIOR
Solitary, nocturnal hunter that prowls slow-moving streams, lakes, and swamps. During the daytime it rests at the bottom, taking cover among rocks, woody debris, or vegetation. This may be the typical behavior for most sleepers, hence the common name.

FEEDING ECOLOGY AND DIET
Predaceous; primarily eats small fishes, but also takes crustaceans, insects, and mollusks. Larval fish in culture ponds feed on cladocerans, rotifers, chironomids, and brachiopods.

REPRODUCTIVE BIOLOGY
Reach sexual maturity at approximately 3.9–4.7 in (10–12 cm) standard length. Spawns January through October. The eggs are about 0.09 in (2.3 mm) long and 0.02 in (0.63 mm) wide. Hatching starts at about 41 hours after fertilization, reaching its peak about 60–70 hours after fertilization. The males care for the eggs and guard the newly hatched fry. The larvae are initially pelagic but change to a more benthic habitat after about 25–30 days, becoming quite sedentary after about 40 days.

CONSERVATION STATUS
Not listed by the IUCN, but the species may be declining in some parts of its native range due to overharvesting.

SIGNIFICANCE TO HUMANS
A highly prized food fish in Southeast Asia, where it is also raised in ponds. In 2000, 277 tons (282 t) of marble sleeper were produced by aquaculture in Malaysia, Singapore, and Thailand. This quantity represents about 74% of the total global aquaculture of gobioid fishes for 2000, and had a value of about $1.2 million. In Borneo, marble sleepers captured for markets in Singapore and Japan may bring a fisherman $20 per lb ($10 per kg). ◆

Gorgeous prawn-goby
Amblyeleotris wheeleri

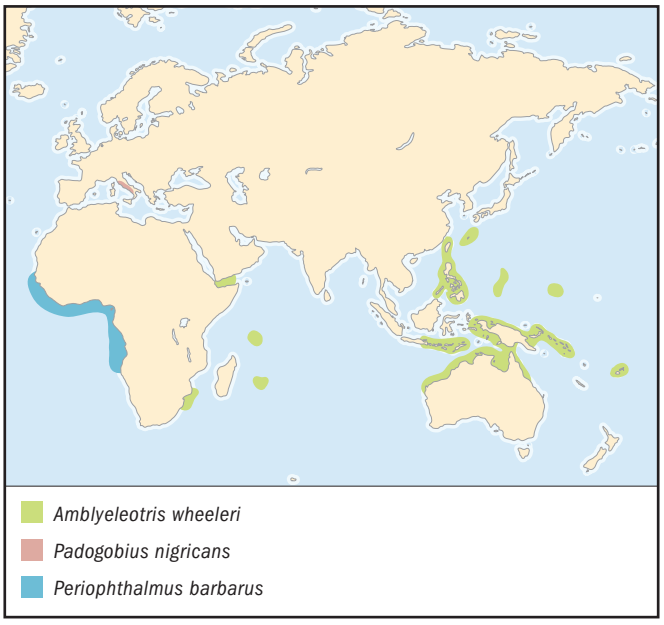
FAMILY
Gobiidae

TAXONOMY
Cryptocentrus wheeleri Polunin and Lubbock, 1977, Aldabra Atoll, Seychelles.

OTHER COMMON NAMES
English: Gorgeous goby, Wheeler's shrimp goby; Afrikaans: Mooidikkop; Gela: Iga taotao; Tagalog: Bia.

PHYSICAL CHARACTERISTICS
Reaches about 3.2 in (8 cm) total length. Body with scales (62–68 in longitudinal series along the flanks). Second dorsal and anal fins, each with 12 soft fin rays. Pelvic fins not forming a strong sucking disk; fins connected between innermost rays but not between spines of each fin. Head and body a light yellowish green or brownish dorsally, with six reddish, vertical, or oblique bands on flanks; numerous small, bluish spots, or reddish spots on head. A vertical red stripe runs from eye to corner of mouth. Fins transparent, and all except pectorals with numerous blue spots and often with reddish bases, and dorsal fins with orange spots near edge. Caudal fin has oblique red stripe.

DISTRIBUTION
Throughout much of the Indo-Pacific region, from East and South Africa and the southern Red Sea to Fiji; in the Pacific, north to Taiwan, and the Ryukyu Islands of southern Japan, and south to the Great Barrier Reef



HABITAT
Lives on sand and rubble patches of reef flats between 16 and 98 ft (5–30 m) deep. Found in association with alpheid prawns (usually *Alpheus ochrostriatus*) that live in burrows.

BEHAVIOR
Typical of several species of gobies that live symbiotically with prawns. The goby rests just outside the prawn's burrow, and retreats into the burrow at the approach of danger. The goby and prawn may stay in reasonably close contact with each other when either leaves the burrow. The goby benefits from the shelter afforded by the burrow, and might also be "cleaned" by the prawn. The goby acts as a "watchman" for the prawn. The goby can signal the presence or absence of danger by flicking movements of its tail, and the prawn feels these signals through its antennae, which it places on the goby's tail. If the prawn cleans the goby of small particles attached to its body, then this may provide a useful food source for the prawn.

FEEDING ECOLOGY AND DIET
Nothing known.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Commercial importance in the aquarium trade. ◆

Whip coral goby
Bryaninops yongei

FAMILY
Gobiidae

TAXONOMY
Cottogobius yongei Davis and Cohen, 1969, Darvel Bay, west of Tatagan Island, Borneo.

OTHER COMMON NAMES
Japanese: Garasuhaze; Samoan: Mano'o.

PHYSICAL CHARACTERISTICS
Small, reaches about 1.2 in (3 cm) standard length. The preoperculum has a slightly scalloped edge, visible just behind the mouth. Body with scales (26–58 in longitudinal series along the flanks). The pelvics form a small suctorial disk. The head is transparent except for some brownish patches on the sides, a distinct reddish gold stripe that extends dorsally around the snout, and some reddish spots and a band over the top of the head. The eyes are bright golden with reddish rims. The body is transparent, with about six darkish or reddish brown bands on flanks. The ventral part of the body is mottled brown, and there is a large brown or reddish patch at the base of the pectoral fin. The dorsal, anal, and caudal fins may be reddish.

DISTRIBUTION
From the Red Sea, to the Seychelles in the Indian Ocean. More common in the Pacific Ocean from Indonesia east to French Polynesia, north to Hawaii and southern Japan, and south to the Great Barrier Reef.

HABITAT
Apparently restricted to small patches that are widely dispersed. The fish live only on the sea whip (*Cirripathes anguina*), found on drop offs in strong currents and on sheltered back reefs, from 9.9 to 148 ft (3–45 m) deep.

BEHAVIOR
Small sea whips are occupied by a single immature fish. Larger sea whips are occupied by a male-female pair. Juveniles and a second small female may also be present.

FEEDING ECOLOGY AND DIET
Nothing known.

REPRODUCTIVE BIOLOGY
The male-female pair on the sea whip are probably monogamous. About 6–8 in (15–20 cm) in from the tip of the sea whip, the fish clear living tissue from the whip in a narrow band about 0.9 in (23 mm) wide, exposing the underlying skeleton. The eggs are attached in a wide band over this "nest." Individual fish can change sex, apparently either way. The largest female to settle on a whip might become a male and the next largest fish remain a female, thus forming a pair. Fish that lose their mates might revert to a bisexual state, allowing them to mate with any fish of either sex that subsequently settles on the sea whip.

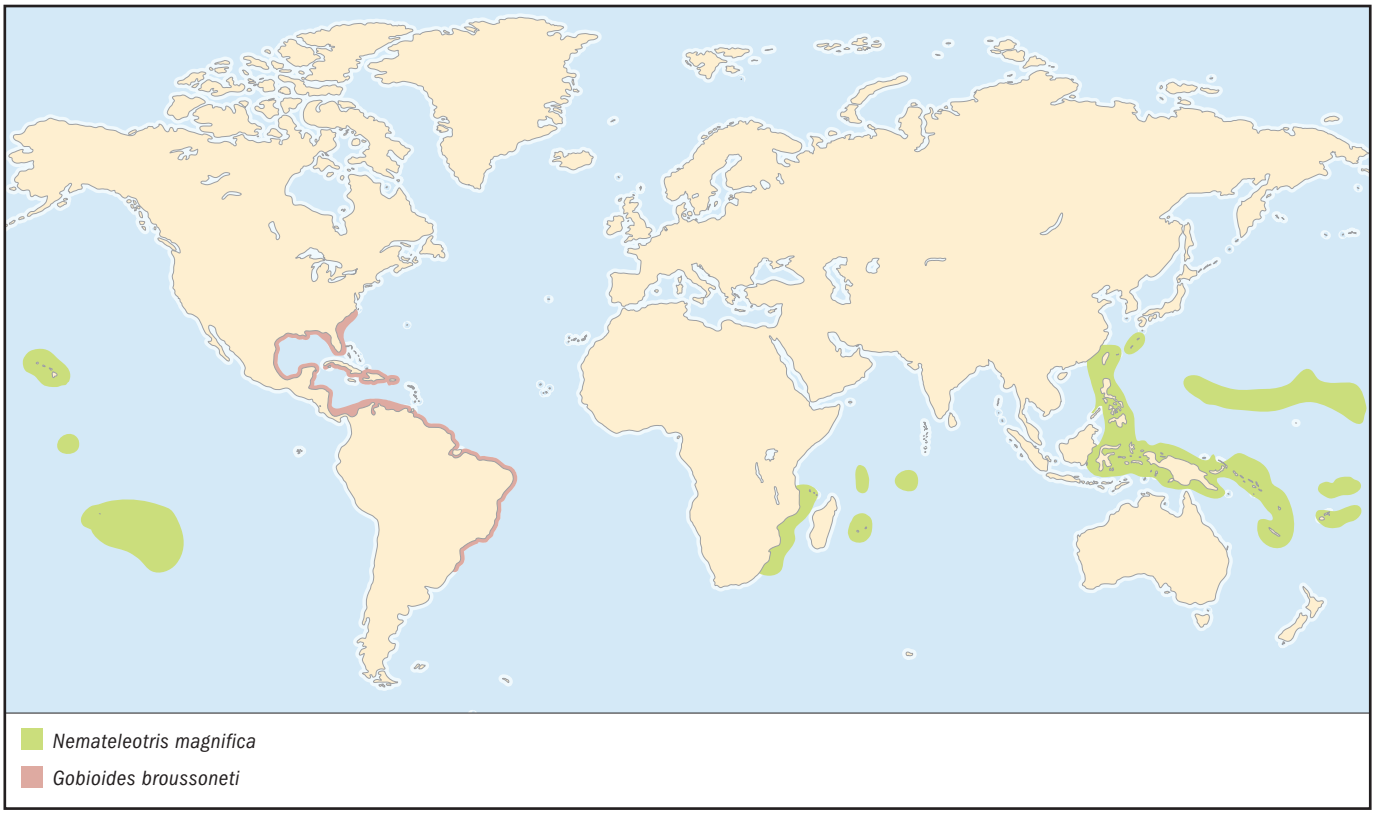
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Found in the aquarium trade, but not common. ◆

Violet goby
Gobioides broussoneti

FAMILY
Gobiidae

TAXONOMY
Gobioides broussonnetii Lacepede, 1800, Suriname.



OTHER COMMON NAMES
German: Lila Aalgrundel; Spanish: Lamprea; Portuguese: Aimore.

PHYSICAL CHARACTERISTICS
To about 21.6 in (55 cm) total length. The body is elongate and eel-like. Dorsal fins united to form a long continuous fin confluent with the caudal fin. Anal fin also connected to caudal fin. The caudal fin is long and pointed. Pelvic fins are united to form a concave disk. The mouth is large and oblique. The eyes are small and high on the head. The body and head are purple brown, the abdomen and underside of the head are white. A series of dark chevrons, angled forward, extends along the sides.

DISTRIBUTION
Western Atlantic, Gulf and Caribbean coasts of the Americas, extending from Brunswick County, North Carolina, to Rio Grande do Sul, Brazil. Also on coasts of Cuba, Hispaniola, and Puerto Rico in the Caribbean.

HABITAT
Lives on muddy bottoms and in burrows; inhabits tidal freshwater and low salinity estuaries offshore from large rivers; one individual was found 298.5 ft (91 m) off the Mississippi River in Louisiana.

BEHAVIOR
No published information is available, but some is forthcoming from the aquarium trade. Males display for females before spawning by raising and lowering the dorsal fin, and swimming in and around the potential nest site. Males become territorial after spawning and guard the nest.

FEEDING ECOLOGY AND DIET
The long coiled gut suggests that it feeds on diatoms, algae, and tiny invertebrates sifted from sediments.

REPRODUCTIVE BIOLOGY
In the aquarium, spawning may last 12–24 hours. Eggs are deposited in nests under an object, presumably within a burrow in the wild. Eggs hatch in 36–38 hours. Males usually guard the fry until they swim freely.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No commercial fishing values, but becoming an increasing part of the aquarium trade because of its interesting appearance. ◆

Neon goby
Gobiosoma oceanops

FAMILY
Gobiidae

TAXONOMY
Elacatinus oceanops Jordan, 1904, Garden Key, Tortugas, Florida.

OTHER COMMON NAMES
English: Blue neon goby.

PHYSICAL CHARACTERISTICS
Small, slender goby with an pointed, bulbous snout. Maximum length about 2.4 in (6 cm). Has two dorsal fins and a square-shaped caudal fin about the same height as the body. The pelvic fins are joined to form a cuplike sucking disk. Dorsally the fish is dark, with an iridescent pale blue stripe running laterally along the lower edge of the dorsum, extending from the snout to the caudal fin. This lateral streak in fishes from Belize is blue in the middle bordered by white. The underside of the head and the abdomen are pale.

DISTRIBUTION
Southern Florida, the Flower Garden coral reefs 100 mi (161 km) off the Texas-Louisiana border, Alacran Reef of northern Yucatán, Quintana Roo state (Yucatán peninsula of Mexico), and Belize.

HABITAT
Inhabits coral reefs and tropical rocky substrates at depths from 3.3 to 131 ft (1–40 m). Has also been observed associated with large sponges.

BEHAVIOR
Rests on coral and withdraws into crevices when threatened. A cleaner goby that picks parasites off other fishes, the male cleans the undersides of rocks, corals, or shells to prepare the surface for eggs.

FEEDING ECOLOGY AND DIET
This is a cleaner goby that picks parasites off other fishes. As with other cleaner gobies, this species waits for other fishes at stations on top of coral heads. It will then swim along the fish and remove ectoparasites from its skin. Its diet includes parasites, fish scales (perhaps accidentally removed), and benthic invertebrates. Larvae feed on small plankton.

REPRODUCTIVE BIOLOGY
Males clean the undersides of rocks, corals, or shells to prepare the surface for eggs. The male swims in front of the female and entices her into the shell or crevice. Spawning occurs with the male and female quivering side-by-side, depositing the eggs on the ceiling of the nest. Individuals can spawn multiple clutches, several times within a month. The eggs are about 0.08 in (2 mm) long, and 0.04 in (1 mm) wide. About 300–450 eggs are deposited in a nest about 0.5 sq in (3 sq cm). The pair remains together while caring for the eggs. The male guards the nest and presumably circulates oxygen-rich water over the eggs, using his pectoral and caudal fins. Eggs hatch in 7–10 days. Larvae are 0.16 in (4 mm) at hatching, and the parents do not care for the fry.

CONSERVATION STATUS
Not threatened.

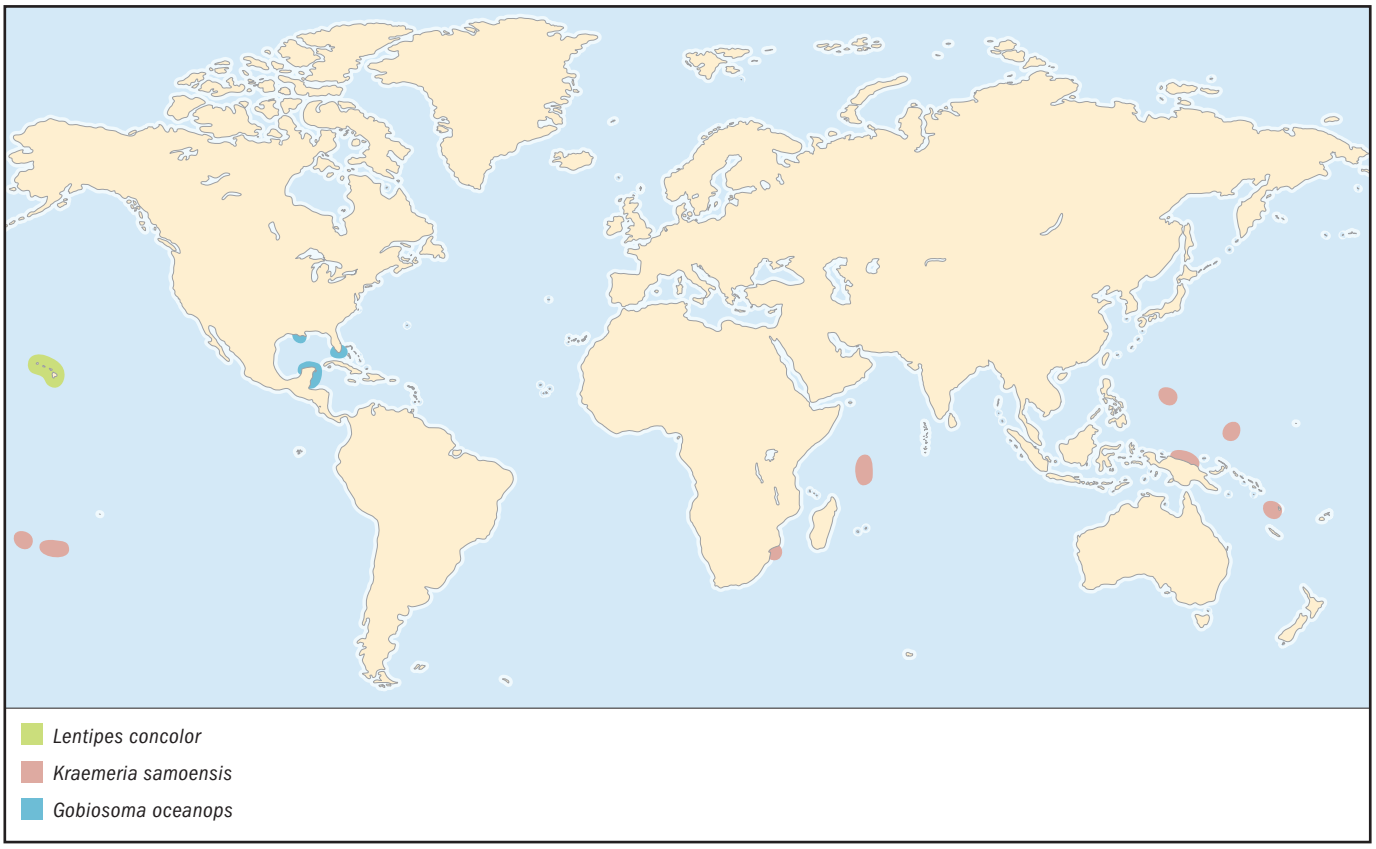
SIGNIFICANCE TO HUMANS
This colorful fish is a popular, nonaggressive aquarium species that does not require much space. It is commercially important in the saltwater aquarium trade. ◆

O'opo alamo'o
Lentipes concolor

FAMILY
Gobiidae

TAXONOMY
Sicyogaster concolor Gill, 1860, Hilo, Hawaii. Part of the subfamily Sicydiinae.

OTHER COMMON NAMES
Hawaiian: 'alamo'o.



PHYSICAL CHARACTERISTICS
To 5.3 in (13.4 cm) total length. A tubular species with a blunt head, subterminal mouth, and rounded caudal fin. Pelvic fins are united to form a cup and adhere to the body. Gray or brownish trunk with irregular lateral markings that sometimes form bands. Breeding males transform from the drab color to black on the anterior half of the body, and red or white tinged with red posteriorly, with white median fins.

DISTRIBUTION
Hawaiian Islands.

HABITAT
Adults and juveniles ascend waterfalls to inhabit headwaters and upper reaches of perennial rain-forest streams on the high islands of the Hawaiian archipelago. It has been reported from sites as high as 2,947 ft (900 m) above sea level. This species has planktonic marine larvae.

BEHAVIOR
Larvae of this amphidromous species wash out to sea where they may remain for a period of three months. Post-larvae return to fresh water, and ascend waterfalls to colonize the upper reaches of streams; sicydiine gobies probably use their pelvic fins and their teeth to gain purchase on the rock surface as they climb waterfalls. Genetic evidence suggests that they do not return to the natal stream.

FEEDING ECOLOGY AND DIET
Predominantly herbivorous, has rows of fine teeth that are ideal for scraping algae from the surface of rocks in the stream bed. As the old teeth break or wear down, they are replaced by fresh teeth. Freshwater shrimps are also taken in small numbers.

REPRODUCTIVE BIOLOGY
Breeds from October through June. Males may establish and patrol reproductive territories, but evidence for this is inconclusive. Males defend nest cavities prior to breeding and pair with females prior to spawning for two to six days. Spawning may last several hours, during which females deposit eggs on the underside of the roof of the nest cavity before being chased out by the male. Individual females may spawn four clutches a season, with an average of nearly 14,000 eggs. After spawning, males apparently guard the nests. Although not directly observed, males may also clear detritus from nest cavities. Eggs hatch in three to six days.

CONSERVATION STATUS
Not currently threatened; classified as Data Deficient by the IUCN. This species was listed as a Category 1 candidate for Endangered Species classification by the U.S. Fish and Wildlife Service from 1989 to 1996. It was removed from the list when it was discovered to be more widely abundant than previously believed. Many populations were not identified prior to listing, in part because upstream sites were undersampled.

SIGNIFICANCE TO HUMANS
No commercial value. ◆

Arno goby
Padogobius nigricans

FAMILY
Gobiidae

TAXONOMY
Gobius fluviatilis var. *nigricans* Canestrini, 1867, Arno River, Italy.

OTHER COMMON NAMES
Italian: Ghiozzo di ruscello.

PHYSICAL CHARACTERISTICS
Males reach slightly beyond 4.9 in (12.5 cm) total length. Tubular species with a blunt head and terminal mouth. Two dorsal fins, second with 12–14 fin rays. Rounded caudal fin. Pelvic fins form a sucking disc, which does not extend as far as the anus. There are 44–49 ctenoid scales along the midline of the flanks. Brownish or light brown dorsally, and whitish ventrally. Five characteristic brown bands over the back, the first at the base of the pectoral fin and the last at the caudal peduncle. Dorsal fins with alternating light and dark gray bands; the first dorsal fin has a yellowish orange border.

DISTRIBUTION
Formerly widespread through fresh waters of central Italy. Currently found in the Serchio, Arno, Ombrone, and Tiber River basins. Populations have become restricted because of environmental degradation and pollution.

HABITAT
Small to medium-sized streams with moderate current. Usually found in clear waters, over a stony substrate.

BEHAVIOR
Usually stationary, positioned under stones, occasionally moves quickly from one stone to another.

FEEDING ECOLOGY AND DIET
Predaceous; feeds on oligochaetes, crustaceans, and insect larvae.

REPRODUCTIVE BIOLOGY
Probably reaches sexual maturity during the first year, at 1.6–2 in (4–5 cm). Males become very dark during the reproductive period, which usually occurs between May and June. The male is territorial and guards a nesting cavity under a stone, attracting females with a courtship display and making noises as he does. The male carries small stones out from the nest in his mouth and deposits them near the female, and then quickly returns to the nest. He repeats this behavior until the female enters the nest, and then swims several times upside down over the roof of the nest. The female attaches herself to the roof of the nest using the pelvic disk and spawns 100–200 eggs, which are stuck to the roof. Several females can spawn in the same nest, which may hold over 1,500 eggs at various stages of development. The male cares for the eggs until they hatch, after about 17 days.

CONSERVATION STATUS
Listed as Vulnerable by the IUCN, with a suspected population reduction of at least 20% over the last 10 years, or three generations. Populations are threatened by environmental degradation and, in some areas, by the introduction of *Padogobius martensii*, which probably competes for similar ecological niches.

SIGNIFICANCE TO HUMANS
There is no commercial or sports fishery for this species. However, the flesh tastes good and fishes are collected illegally and eaten fried. ◆

Dwarf pygmy goby
Pandaka pygmaea

FAMILY
Gobiidae

TAXONOMY
Pandaka pygmaea Herre, 1927, Philippines (possibly Malabon).

OTHER COMMON NAMES
German: Zwerggrundel; Tagalog: Bia.

PHYSICAL CHARACTERISTICS
A very small fish; females reach 0.6 in (1.5 cm) total length. Body is covered with scales, up to 25 in a longitudinal series along the flanks. The second dorsal and anal fins have six or seven soft rays. The pelvic fins are united into a small sucking disk. The body has a conspicuous pigmentation, with about four cross bands of dark spots on the flanks, and heavy pigmentation on the bases of all the fins except the pelvics. In males, the first dorsal fin is tipped with blue and the lower third is yellowish.

DISTRIBUTION
First reported as possibly from Malabon, a suburb of Manila in the Philippines. The presence of the species in the Malabon River was confirmed in the 1950s. Subsequently, it has been found at an island off Palawan (Philippines), the east coast of peninsular Thailand, Singapore, Bali, Sulawesi, and New Guinea.

HABITAT
Found along river banks in the Philippines from January to June, when the water is clear and the tide is rising. During the rainy season the fishes apparently move into ponds and canals. Also found in brackish waters and around mangroves. Some specimens were apparently caught in marine waters adjacent to Palawan. Fishes kept in aquaria can acclimate to marine, brackish, or freshwater conditions.

BEHAVIOR
Usually stationary, on surfaces of rocks or plants, or hanging in midwater. Swimming occurs in an erratic series of starts.

FEEDING ECOLOGY AND DIET
Aquarium-kept specimens are voracious, feeding on brine shrimps and other small or chopped invertebrate material.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Listed as Critically Endangered by the IUCN, with an observed or suspected population reduction of 90% or more over the last 10 years, or three generations. Populations are threatened by introduced species, hybridization, pathogens, pollutants, competitors, or parasites.

SIGNIFICANCE TO HUMANS
None known. ◆

Atlantic mudskipper
Periophthalmus barbarus

FAMILY
Gobiidae

TAXONOMY
Gobius barbarus Linnaeus, 1766, Liberia. Based on a neotype specimen designated in 1989.

OTHER COMMON NAMES
French: Sauteur de vase atlantique; German: Schlammspringer; Spanish: Saltafango atlantico; Akan: Soetsi; Portuguese: Saltao-da-vasa.

PHYSICAL CHARACTERISTICS
To about 6 in (15 cm) total length. Prominent eyes with ventral eyelids perched on top of large head. Two dorsal fins. Muscular pectoral fin and pelvic fin bases used for crawling and climbing. Pelvic fins separate. Body tan but light ventrally, and with black diagonal bars dorsally on flanks; opalescent spots on head and anterior trunk; light margin on first dorsal fin may be tinged with light blue, lower portion dark; second dorsal fin with dark submarginal band over a light band.

DISTRIBUTION
West African coast from Senegal to Angola, including most islands.

HABITAT
Inhabits the littoral zone of mangrove estuaries and muddy intertidal flats where it lives in burrows.

BEHAVIOR
Amphibious; lives in burrows in the mangal zone. Territorial, forages for food on the mudflats and around the mangroves themselves. They can flee predators by skipping or hopping across the flats and into the mangrove forests or into their burrows. When on land, mudskippers keep a mouthful of water for extracting oxygen via the gills, and they can breathe through the skin which is well served with blood vessels.

FEEDING ECOLOGY AND DIET
Eats crustaceans, worms, and insects from the intertidal zone.

REPRODUCTIVE BIOLOGY
Reproduction occurs in burrows.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
No commercial fishing value; plays a minor role in the aquarium trade. ◆

Samoan sand dart
Kraemeria samoensis

FAMILY
Kraemeriidae

TAXONOMY
Kraemeria samoensis Steindachner, 1906, Samoan Islands.

OTHER COMMON NAMES
English: Sand dart; Afrikaans: sandspies.

PHYSICAL CHARACTERISTICS
Small, elongate fish, reaches 1.4 in (3.5 cm) total length. Lacks scales. Head with minute eyes, and a "chinlike" forward projection of the lower jaw. Six or seven small flaps project from the lower edge of the preoperculum, just behind the mouth, and five or six flaps project from the lower edge of the operculum covering the gills. There is a single, long, dorsal fin, and a long anal fin. Specimens from the Indian Ocean have fewer opercular flaps than those from the Pacific, and might represent a different species.

DISTRIBUTION
The Indo-Pacific region, from East Africa to the Society Islands.

HABITAT
Buries into loose coral sand in inshore areas where there is strong wave action.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Feeds on polychaetes.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Fire goby
Nemateleotris magnifica

FAMILY
Ptereleotridae

TAXONOMY
Nemateleotris magnificus Fowler, 1938, Buka Buka Island, Gulf of Tomini, Sulawesi, Indonesia.

OTHER COMMON NAMES
English: Fire dartfish, firefish; French: Gobie de feu; Afrikaans: Vuur-dikkop; Japanese: Hatatatehaze; Malay: Roket antene; Samoan: Mano'o-sugale.

PHYSICAL CHARACTERISTICS
Maximum size 3.5 in (9 cm) total length. This is one of the "hovering" gobies, a species that actually hovers in the water column instead of hugging the bottom like most of its kin. The body form is more compressed laterally (deeper and thinner) instead of the more typical tubular goby shape. The anterior portion of the first dorsal fin is greatly elongate, almost as long as the fish itself in some specimens. The pelvic fins are separate. The second dorsal and anal fins are long and, when extended, have the appearance of a feather, or the tail end of an arrow or a dart. The fish has a rounded caudal fin. The head has a yellow mask over the snout and eyes. The front half of the fish (other than the mask) is white, the back half grades from orange to red, with green streaks in the median fins converging posteriorly.

DISTRIBUTION
Tropical Indian and Pacific Oceans, from South Africa to the Marquesas. In the Pacific, extends north to the Hawaiian and Ryukyu Islands, and south to New Caledonia.

HABITAT
Coral-reef species found on the upper slopes of the outer reef. Although observed at depths from 20–200 ft (6–61 m), it is usually found at less than 92 ft (28 m). Creates burrows to which it can retreat when threatened.

BEHAVIOR
Occurring singly or in small group, this species hovers in the water column, a few centimeters above sand or rubble, selectively feeding on drifting zooplankton. Usually has a small territory around a hole, cave, or burrow into which it retreats at

the threat of danger. The burrow may be shared. Has a habit of flicking the first dorsal spine up and down, erecting the dorsal fin when threatened or defending territory.

FEEDING ECOLOGY AND DIET
Feeds on zooplankton, including crustacean larvae and copepods.

REPRODUCTIVE BIOLOGY
Spawning occurs in burrows.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
This beautiful fish is an important saltwater aquarium species. ◆

Loach goby
Rhyacichthys aspro

FAMILY
Rhyacichthyidae

TAXONOMY
Platyptera aspro Valenciennes, 1837, west Java and Sulawesi. Although *Rhyacichthys aspro* has several specializations of its own, it is considered to be a primitive representative of the Gobioidei.

OTHER COMMON NAMES
Ilokano: Kampa; Japanese: Tsubasahaze; Visayan: Dalapakan.

PHYSICAL CHARACTERISTICS
Reaches 12.6 in (32 cm) total length. Head depressed dorsally, with a wedgelike snout, and with small eyes. Mouth ventrally placed on head with a fleshy upper lip. Body laterally compressed toward tail, which is slightly forked; body with 27–40 scales in longitudinal series on flanks. Lateral line system well developed on head and body. Pelvic fins separate, each with a patch of enlarged musculature on the anterior border. Body light brown with several darker, longitudinal stripes on flanks; dark bands running from eye toward anterior tip of snout. Dorsal fins with alternating light and dark longitudinal stripes; caudal and pectoral fins pale with several dark vertical bands.

DISTRIBUTION
Islands of the western Pacific rim, extending in an arc from the Ryukyu Islands of southern Japan, through Taiwan, Indonesia, and the Philippines, to New Guinea and the Solomon Islands.

HABITAT
Clings to rocks and boulders in fresh waters of torrential hill streams. The streamlined head and body shape makes this species well suited to living in these fast-flowing waters. The fish may use the ventral part of head, thoracic region of the body, and the pectoral and pelvic fins to attach to rocks. This might be done by friction between the rock surface and rough surfaces on the underside of the body, or by suction, in which a low-pressure water flow between the body and the rock "sticks" the fish to the substrate.

BEHAVIOR
Swims in a series of rapid darts and, at the approach of danger, quickly moves into crevices under large rocks or boulders.

FEEDING ECOLOGY AND DIET
Herbivorous, browses on algae on the surfaces of stones.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

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Acanthuroidei
(Surgeonfishes and relatives)

Class Actinopterygii
Order Perciformes
Suborder Acanthuroidei
Number of families 6

Photo: A yellowtailed surgeonfish (*Prionurus laticlavius*) school swims over the lava bottom of the Roca Redonda, Galápagos Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permsiion.)

Evolution and systematics

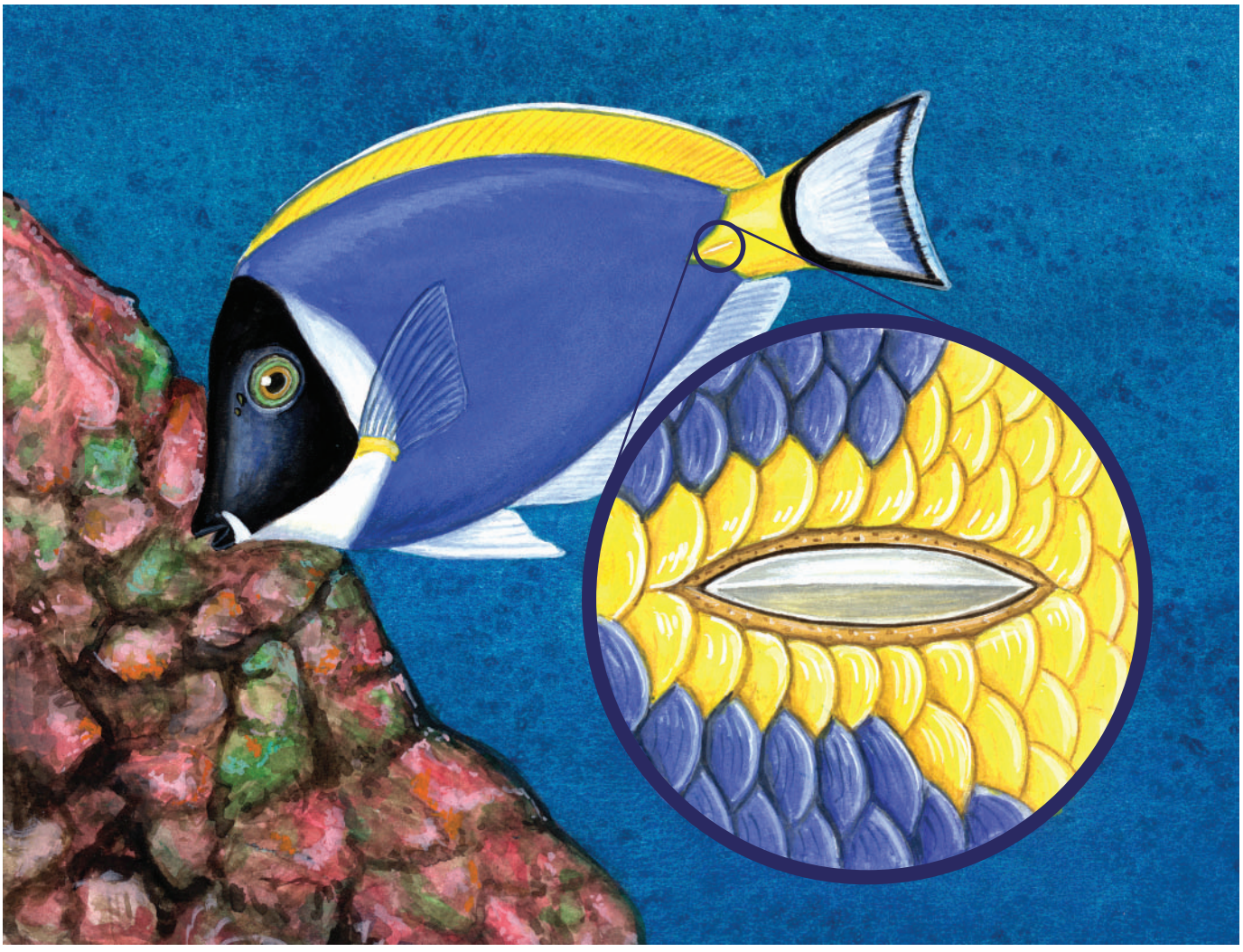
The suborder Acanthuroidei comprises six families and 128 species. The families are Ephippidae (spadefishes, or batfishes, with eight genera and 15 species), Scatophagidae (scats, with two genera and four species), Siganidae (rabbitfishes, or spinefoots, with one genus, two subgenera, and 27 species), Luvaridae (louvar, with one genus and one species), Zanclidae (Moorish idol, with one genus and one species), and Acanthuridae (surgeonfishes and tangs, with six genera and 80 species). Some researchers also place the Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), and Drepaneidae (sicklefishes) in this suborder on the basis that these fishes are sister taxa to the acanthuroid fishes. This view is not accepted universally, and so these three families are treated elsewhere in this volume.

The Ephippidae and Scatophagidae date from the Lower Eocene, while the Siganidae, Zanclidae, and Acanthuridae are from the Middle Eocene. The origin of the Luvaridae is uncertain. The suborder is considered to be monophyletic, with or without the inclusion of the Chaetodontidae, Pomacanthidae, and Drepaneidae. One feature common to half the members of this suborder is the presence of sharp, venomous spines (Scatophagidae and Siganidae) or sharp peduncular spines or keels (Acanthuridae), which also may be venomous.

Physical characteristics

All but one species in this suborder have small to medium-size bodies that are compressed and may be deep, disc-like, ovate, or slightly elongated. The spadefishes, or batfishes (Ephippidae), have deep and highly compressed bodies, continuous dorsal fins, and highly elevated dorsal, anal, and pelvic fins. Their scales are small and ctenoid, and their mouths are small and terminal. The scats (Scatophagidae) have deep, compressed bodies, a pronounced forehead, a mouth that is nonprotrusible, and a deeply notched dorsal fin. Fin spines are sharp and reportedly venomous. The rabbitfishes, or spinefoots (Siganidae), have compressed, somewhat elongated bodies; some in the subgenus *Lo* have a pronounced snout. Siganids are distinguished by the presence of venomous fin spines. Color patterns vary, and some species are quite distinctive. The monotypic louvar (Luvaridae) has a large (up to 78.7 in, or 200 cm, in length) fusiform body that is slightly compressed and quite streamlined. The head is blunt, with a projecting forehead; the mouth is small and somewhat protrusible; and the opercular spines are flattened. There is a groove positioned just above the eye. There are no pelvic fins, and the caudal peduncle has a large keel and small accessory keels. The scales are dentroid and quite small. Maximum body sizes range from 6–36 in (15–91 cm) for spadefishes and batfishes, 3.5–16 in (9–40 cm) for scats, 8.5–21 in (22–53 cm) for rabbitfishes and spinefoots, and 6.3–39.5 in (16–100 cm) for surgeonfishes. Moorish idols reach about 9 in (23 cm), and louvars reach about 79 in (200 cm) in length.

The Moorish idol (Zanclidae) is also monotypic within its family. This distinctive species has a disc-like body that is strongly compressed and dorsal spines that form an elongated whiplike streamer or filament. The color pattern is a striking arrangement of yellow, black, and white. Surgeonfishes (Acanthuridae) have compressed and disc-like bodies and possess one or more scalpel-like caudal spines or keeled peduncular plates located on each side of the caudal peduncle, which vary in size with species, may be venomous, and are capable of inflicting a painful, if not serious, wound. The caudal fin is strongly lunate, emarginate, or truncate. Many species are quite colorful, whereas others are seemingly drab until close inspection reveals often minute but exquisite details.



Detail of sharp scapel (modified spine) on caudal peduncle of a powder blue tang (*Acanthurus leucosternon*). (Illustration by Joseph E. Trumpey)

Distribution

Five of the six families are distributed in continental and insular inshore habitats of tropical, subtropical, and warm temperate seas. The exception is the louvar, a species that is pelagic throughout its rather wide range. Spadefishes, or batfishes, and surgeonfishes occur in the Atlantic, Indian, and Pacific Oceans. Scats are limited to the Indo-West Pacific, whereas the Moorish idol is found there and in the eastern Pacific. Rabbitfishes occur in the Indo-West Pacific but also have colonized the eastern Mediterranean, via the Suez Canal.

Habitat

All but the louvar, which is pelagic, inhabit shallow coral and rocky reefs, although some species inhabit estuaries or even freshwater habitats. Spadefishes and batfishes favor marine coral and rocky reefs as well as brackish water habitats that include mangroves, sea grasses, or sand and rubble flats. The scats have the greatest flexibility, moving from coral and rocky reefs into brackish water estuaries and freshwater streams. Rabbitfishes also are found on coral (some exclusively) or rocky reefs, on algal or sea grass beds, or around mangroves, but some enter brackish waters. Louvars move up and down in the pelagic water column. The Moorish idol is found on coral or rocky reefs, as are the surgeonfishes, although the latter also may occur on sea grass and algae beds and around mangroves.

Behavior

All members of this suborder except one may be found singly, in small groups, or in aggregations, schools, or mixed-species schools. The exception is the louvar, a solitary fish that probably aggregates only to breed. Many of these fishes, including some rabbitfishes and surgeonfishes, are territorial. Others, such as some rabbitfishes, patrol home ranges in pairs. Numerous species of rabbitfishes also have post-larvae that often form large schools when they settle onto reefs as post-larvae and recruit into (join) the population as juveniles. Batfishes tend to hover singly or in small groups near structures but can form large schools in deeper water as well. Their juveniles mimic fallen leaves. Scats also move about

A school of blue tangs (*Acanthurus coeruleus*) eating the eggs of a sergeant major near the Saba Island of the Netherland Antilles. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

near shelter but form larger aggregations in estuaries, bays, or open water.

Feeding ecology and diet

Spadefishes, or batfishes, are omnivorous and feed on benthic algae and invertebrates. Some species are capable of crushing bivalve or gastropod shells and crustaceans. Although scats have markedly herivorous tendencies, they are also known to be omnivorous; they even feed on detrital materials and have been observed to feed on feces discharged by ships or sewage systems. Aquatic macrophytes consitute the bulk of the stomach contents of both *S. argus* and *S. tetracanthus* in freshwater habitats. Rabbitfishes are herbivorous or omnivorous, and schools of juveniles are efficient, if not rapid, grazers. The louvar feeds on gelatinous mesoplankton in the water column. The Moorish idol feeds primarily on sponges but also plucks other benthic invertebrates. Surgeonfishes are largely herbivorous and browse or graze on benthic algae. Some species are adapted to feeding on plankton in the water column.

Reproductive biology

Almost all members of this suborder spawn pelagic eggs. The exceptions appear to be the scats, which spawn demersal eggs and engage in parental care, and some of the rabbitfishes, which spawn eggs that sink to the bottom. Mating strategies vary within and between families. Courtship and spawning are accomplished in pairs, in pairs within spawning aggregations, or in groups of varying sizes at spawning aggregation sites. Thus, spadefishes, or batfishes, spawn in pairs and possibly in aggregations. Scats spawn demersal eggs, and at least one species practices parental care. Rabbitfishes of the subgenus *Lo* form relatively long-term monogamous pairs. Others in the family, however, spawn in aggregations, in either short-term pairs or groups. Rabbitfishes have been spawned in captivity, and some species are now important in mariculture. Louvars probably spawn in aggregations in the open sea. Moorish idols spawn in pairs or in pairs within aggregations. Surgeonfishes spawn in pairs, as pairs within aggregations, and in groups. The larvae of many of these fishes are well adapted to a prolonged existence in the open sea.

Conservation status

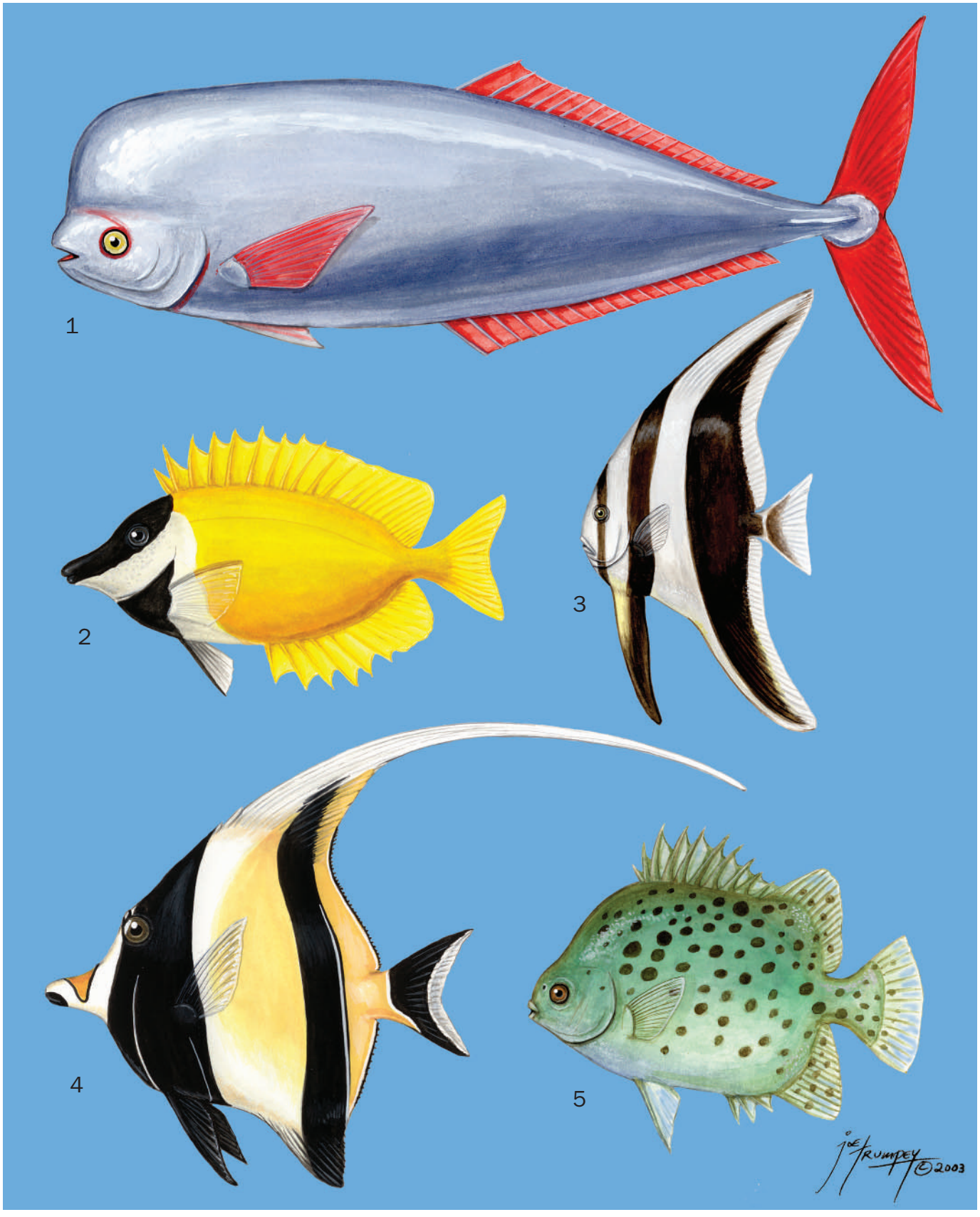
No species is listed by the IUCN, but some species collected for the aquarium trade, including certain surgeonfishes and batfishes, may be at risk locally because of overfishing.

Significance to humans

Rabbitfishes and surgeonfishes are important in subsistence and artisanal fisheries. The louvar is taken as a minor commercial food fish, as are some of the spadefishes, or batfishes. Scats are grown for the live reef food fish trade or taken in subsistence fisheries. Fishes important to the aquarium trade include scats, batfishes, and certain rabbitfishes and surgeonfishes. The Moorish idol also is collected for aquaria, but they do not do well in captivity.

The unusual shape, coloration, and movement of the pinnate batfish (*Platax pinnatus*) probably serve to mimic a toxic flatworm. This is a juvenile batfish swimming near Ambon, Indonesia. (Photo by David Hall/Photo Researchers, Inc. Reproduced by permission.)

1. Yellow tang (*Zebrasoma flavescens*); 2. Striped bristletooth (*Ctenochaetus striatus*); 3. Yellowspotted sawtail (*Prionurus maculatus*); 4. Orangespine unicornfish (*Naso lituratus*); 5. Palette tang (*Paracanthurus hepatus*); 6. Lined surgeonfish (*Acanthurus lineatus*). (Illustration by Joseph E. Trumpey)



1. Louvar (*Luvarus imperialis*); 2. Foxface rabbitfish (*Siganus vulpinus*); 3. Intermediate stage of longfin spadefish (*Platax teira*); 4. Moorish idol (*Zanclus cornutus*); 5. Spotted scat (*Scatophagus argus*). (Illustration by Joseph E. Trumpey)

Species accounts

Lined surgeonfish
Acanthurus lineatus

FAMILY
Acanthuridae

TAXONOMY
Acanthurus lineatus Linnaeus, 1758, "Indies." No type specimens are known.

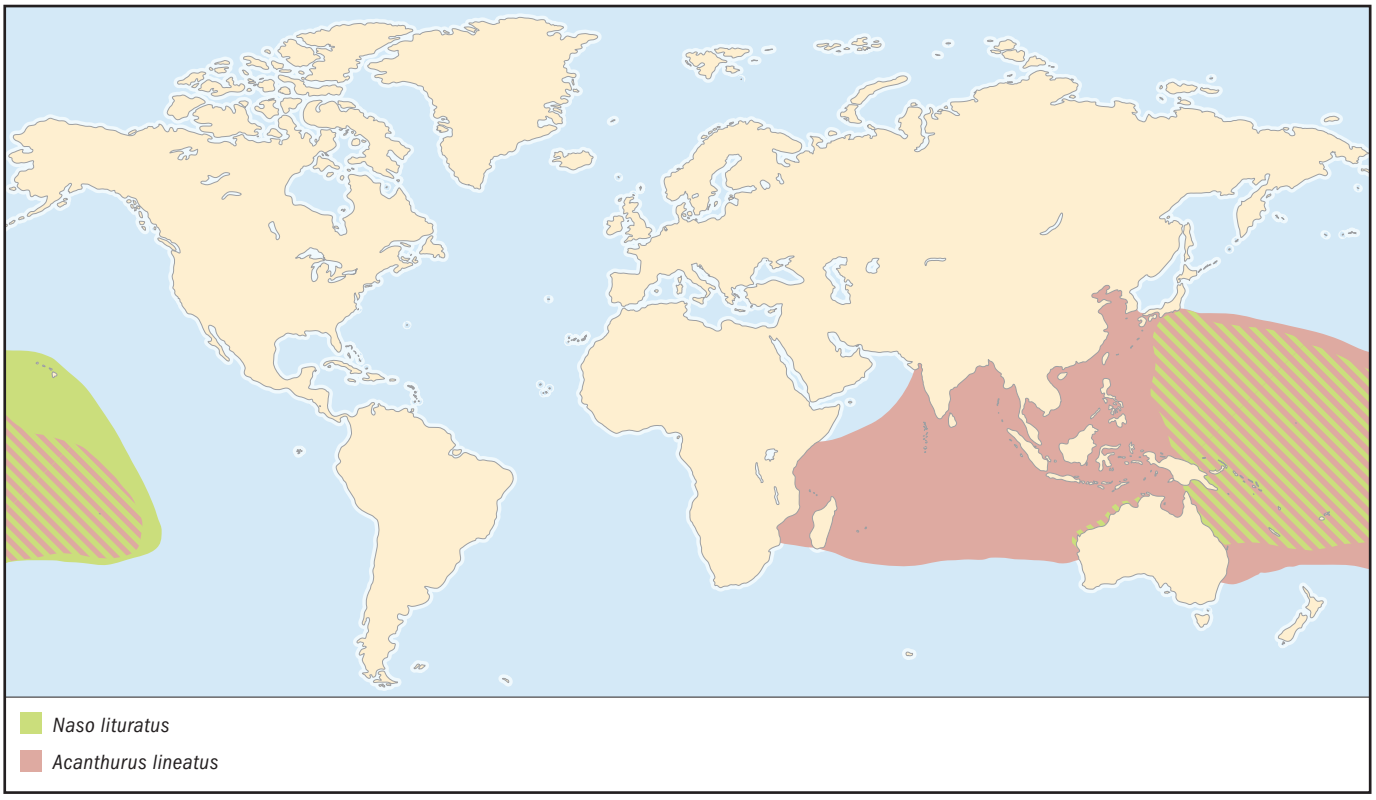
OTHER COMMON NAMES
French: Chirurgien zébré; German: Blaustreifen-Doktosfisch; Japanese: Nijihagi.

PHYSICAL CHARACTERISTICS
The body is compressed and disc-like and possesses a large, venomous, scalpel-like caudal spine on each side of the caudal peduncle. The caudal fin is strongly lunate. There are nine spines and 27–30 soft rays in the dorsal fin, three spines and 25–28 soft rays in the anal fin, and 16 soft rays in the pectoral fin. Body coloration is striking and consists of a yellowish green background, bright blue stripes (narrow and oblique on the head) edged with black on the flank but lacking the black edge on the head, and lavender blue to bluish white on the belly. The pelvic fins are bright orange. The caudal fin has two vertical lines of dark blue set against a background of purplish gray, replaced by yellow at the base of the fin. The remaining fins are purplish gray yielding to greenish yellow at the base. Larvae are acronurus, in that they are orbicular in shape; transparent, with a silvery sheen over the head, chest, and abdomen; and scaleless and have narrow, vertically oriented ridges along the body. (Acronurus refers to the last, well-developed but seemingly different, post-larval stage of surgeonfishes in the genera *Acanthurus*, *Ctenochaetus*, and *Zebrasoma*. Originally this stage was proposed to be a separate genus of surgeonfishes until closer examination revealed otherwise.) The second anal, second dorsal, and pelvic spines are elongated and venomous. Larvae are well adapted to the pelagic realm and may remain there for more than 39 days. Adults may grow to 15 in (38 cm) in length and can live for as long as 30–45 years.

DISTRIBUTION
Indo-West Pacific, from East Africa east to the Marquesas and the Tuamotu Archipelago, north to southern Japan, and south to New South Wales, Australia; strays rarely to the Hawaiian Islands. Replaced by the very similar species *A. sohal* in the vicinity of the Arabian Peninsula (Red Sea and Persian Gulf).

HABITAT
Usually found on exposed reef fronts at depths of 3.3–9.8 ft (1–3 m).

BEHAVIOR
Highly territorial. Patrols territories along the reef front and aggressively attacks conspecifics, other surgeonfishes, and other herbivores. Temporarily assumes a darker coloration of the head during territorial displays and encounters. Wields its caudal spines as effective weapons against attack.



FEEDING ECOLOGY AND DIET
Herbivorous. Browses on filamentous and fleshy algae using specialized teeth.

REPRODUCTIVE BIOLOGY
Migrates to and spawns in aggregations at specific sites, although it sometimes spawns in pairs. Reported to spawn in early morning during the first 1–3 hours of a falling tide just before the full moon. Has been observed spawning at sunset as well. Tidal state, rather than time of day, more likely accounts for the temporal pattern of spawning. Spawning occurs year-round at lower latitudes but may be seasonal at higher latitudes. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An important species in subsistence and artisanal food fisheries. Also collected for larger aquaria. ◆

Orangespine unicornfish
Naso lituratus

FAMILY
Acanthuridae

TAXONOMY
Naso lituratus Forster in Bloch and Schneider, 1801, probably Tahiti, French Polynesia.

OTHER COMMON NAMES
French: Nason a éperon orange; German: Gelbklingen-Nasendoktor; Japanese: Miyako-tenguhagi.

PHYSICAL CHARACTERISTICS
The body is compressed and disc-like, although it elongates with growth. The snout is pronounced, and the forehead slants at a 45-degree angle from just forward of the dorsal fin. The caudal peduncle consists of two peduncular plates, each featuring a large keel facing forward. The caudal fin is emarginate and sexually dimorphic; the males have filaments that trail from each corner of the fin. There are six spines and 28–31 soft rays in the dorsal fin, two spines and 29–31 soft rays in the anal fin, 17–18 soft rays in the pectoral fin, and one spine and three soft rays in the pelvic fin. The body is dark grayish brown with a yellowish patch on the nape, a yellow margin along either side of the snout from the eye to just behind the mouth, a black snout, and an orange mouth. The peduncular plates and keels are bright orange. The dorsal fin is black with a thin blue margin at the base and a broader blue margin along the outer edge. The caudal fin is also black, with a yellow submarginal band on the edge. The anal fin is yellow at the base, followed by an orange band, a narrow submargin of light blue, and a narrow outer margin of black. The pelvic fin is yellow, and the pectoral fin is a faint black. Grows to about 18 in (46 cm) in length.

DISTRIBUTION
Western Pacific, from Surugu Bay, Honshu, Japan, south to the Great Barrier Reef and New Caledonia, and east to the Hawaiian and Pitcairn Islands; recently reported from Clipperton Island in the Eastern Pacific. Also found in the eastern Indian Ocean from the coast of Western Australia south to Ningaloo Reef. Replaced by *N. elegans* in the western Indian Ocean, including southern Indonesia, and the Red Sea.

HABITAT
Coral and rocky reefs in tropical and subtropical waters, generally above 98 ft (30 m) but occasionally as deep as 295 ft (90 m).

BEHAVIOR
Occurs singly or in small groups.

FEEDING ECOLOGY AND DIET
Herbivorous. Browses on benthic algae but favors tough or leafy species from the genera *Sargassum*, *Dictyota*, and *Pocockiella*.

REPRODUCTIVE BIOLOGY
Reported to spawn in pairs but also may spawn in aggregations. Eggs and larvae are pelagic. Larval life is lengthy, in excess of 69 days.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken in subsistence and artisanal fisheries and a popular target of spearfishers. Juveniles and subadults also are collected for the aquarium trade. ◆

Palette tang
Paracanthurus hepatus

FAMILY
Acanthuridae

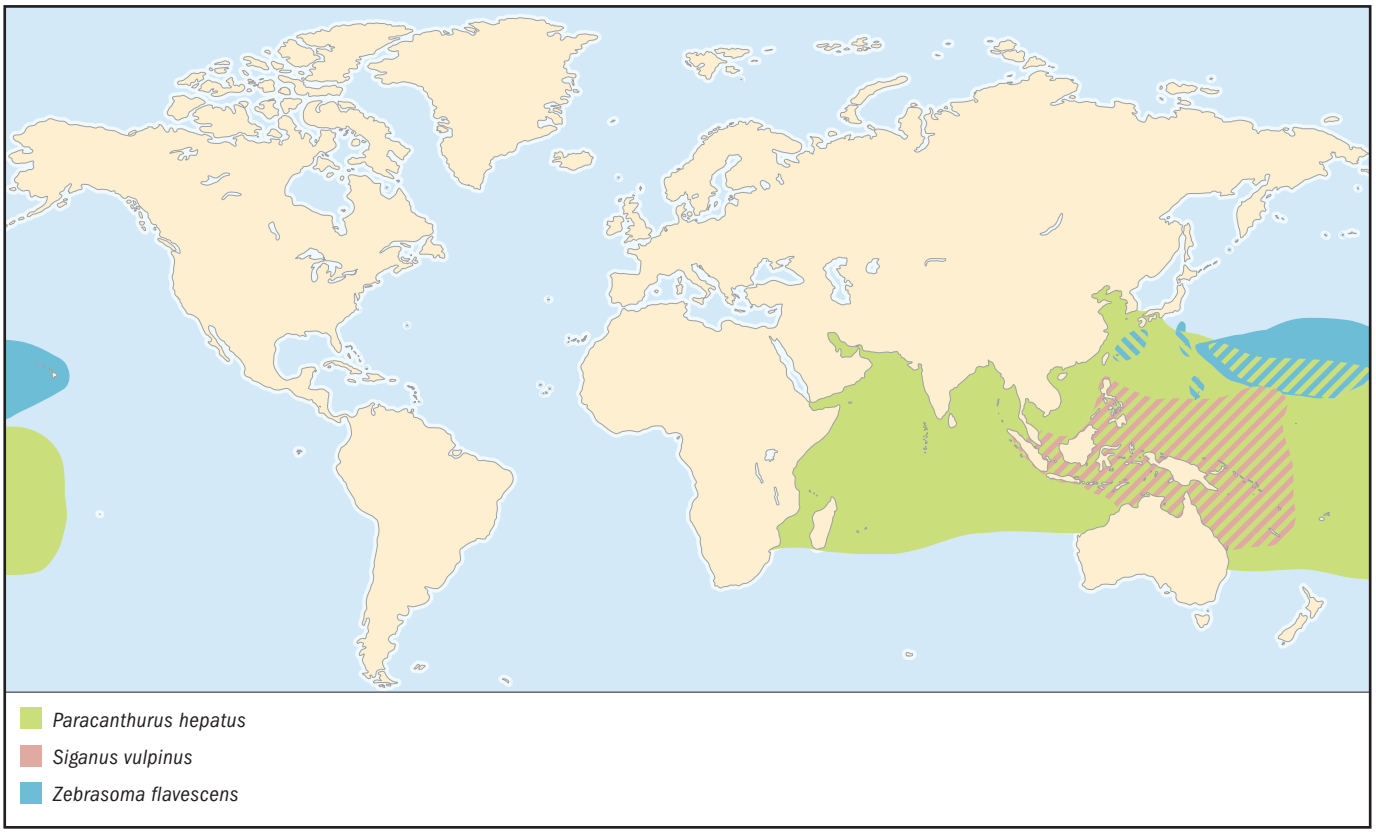
TAXONOMY
Paracanthurus hepatus Linnaeus, 1766, Ambon and Molucca islands, Indonesia. Western Atlantic localities are in error.

OTHER COMMON NAMES
English: Blue tang, hippo; German: Paletten-Doktorfisch.

PHYSICAL CHARACTERISTICS
The body is compressed and somewhat disc-like; it elongates with growth. The caudal fin is truncated in adults, but slightly rounded in juveniles. There are nine spines and 19–20 soft rays in the dorsal fin, three spines and 18–19 soft rays in the anal fin, 16 soft rays in the pectoral fin, and one spine and three soft rays in the pelvic fin. The caudal peduncle has a single folding spine on each side. The body is a vivid bright blue, and the belly is a paler shade of blue or, in Indian Ocean specimens, yellowish blue. A black band curves backward from the eye to the caudal peduncle. A second black band runs back along the middle of the body from just behind the pectoral fin and joins the upper band just before the caudal peduncle. The caudal fin is mainly yellow, the yellow arising just ahead of the caudal spine, with black margins that arise at the caudal peduncle. Grows to 10.2 in (26 cm) in length.

DISTRIBUTION
Tropical and subtropical waters of the Indo-West Pacific, from East Africa east to Micronesia, the Line Islands, and the Samoa Islands, north to Kochi Prefecture in Japan, and south to northern New South Wales, Australia. Observations of this species in Hawaiian Islands are attributed to releases of aquarium stock.

HABITAT
Outer coral and rocky reefs and channels in clear water areas with strong or moderate current. Juveniles and subadults prefer



to shelter in shrublike corals. Not common and patchy in distribution wherever it occurs. Depth range of 6.6–131 ft (2–40 m).

BEHAVIOR
Occurs in small aggregations that hover 3.3–6.6 ft (1–2 m) above the substrate.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on zooplankton and benthic algae.

REPRODUCTIVE BIOLOGY
Reproductive biology is not well known. Courtship probably is paired or paired within a spawning aggregation. Eggs and larvae are pelagic, with a larval life in excess of 37 days.

CONSERVATION STATUS
Not listed by the IUCN. Localized populations are vulnerable to overfishing of juveniles for the aquarium trade.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade, in which it is highly prized. Juveniles and subadults that shelter in corals are relatively easy to collect. ◆

Striped bristletooth
Ctenochaetus striatus

FAMILY
Acanthuridae

TAXONOMY
Ctenochaetus striatus Quoy and Gaimard, 1825, Guam, Mariana Islands.

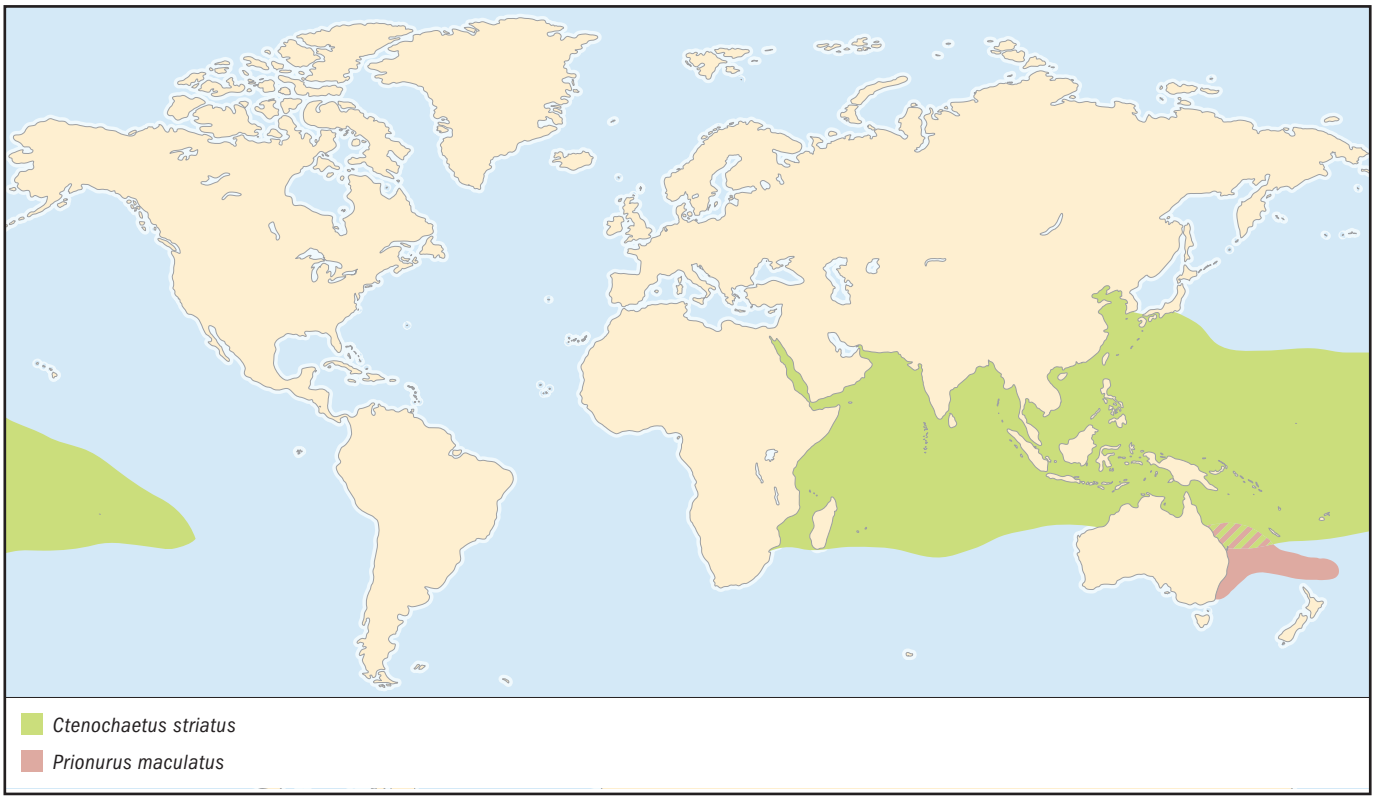
OTHER COMMON NAMES
German: Brauner Borstenzahndoktor; Japanese: Sazanamihagi.

PHYSICAL CHARACTERISTICS
The body is compressed and disc-like, with a venomous, scalpel-like caudal spine on each side of the caudal peduncle. The caudal fin is lunate. There are eight spines and 27–31 soft rays in the dorsal fin, three spines and 24–28 soft rays in the anal fin, and 17 (sometimes 16) soft rays in the pectoral fin. Adult coloration varies from dark gray to orangish brown. Can change color temporarily from dark brown to light tan. Melanistic, albinistic, and xanthic color patterns have been reported as well. There are several fine pale blue lines along the flank. Fine orange spots appear on the upper head and back to the anterior base of the dorsal fin. Both the dorsal and anal fins have narrow dark brown and pale blue bands, running longitudinally in alternation. Juveniles and subadults are especially colorful, with a small black spot located at the posterior base of the dorsal fin. Grows to 10.2 in (26 cm) in length.

DISTRIBUTION
Indo-West Pacific, from the Red Sea south to East Africa, east to Pitcairn Island and French Polynesia (absent from the Marquesas Islands), north to southern Japan, and south to the Great Barrier Reef and New Caledonia.

HABITAT
Found on coral, rock, pavement, and rubble of exposed reefs, reef flats, and lagoons in tropical waters. Depth range from 3.3 to 98 ft (1–30 m).

BEHAVIOR
Found singly but also in small and very large aggregations. Also participates in mixed-species aggregations with other surgeonfishes and parrotfishes, among others.



FEEDING ECOLOGY AND DIET
Herbivorous. Feeds upon benthic algae, blue-green algae, and diatoms. Reported to cause ciguatera poisoning because of their diet. Ciguatera poisoning is caused by the cumulative deposition of a class of polyether toxins within the tissues of fishes. The toxins are produced by certain microscopic dinoflagellate organisms of the genus *Gambierdiscus*, which are transmitted by the food chain, increasing in intensity by a factor of ten in each successive level within the chain. The striped bristletooth ingests these organisms while feeding upon algae. If a contaminated fish is consumed by man, the concentrated poison contained within its tissues causes neurological damage that can be fatal.

REPRODUCTIVE BIOLOGY
Migrates to outer channels or exposed reefs to spawn in aggregations on an outgoing tide. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Taken for subsistence and artisanal food fisheries but may cause ciguatera poisoning at some localities. Also collected infrequently for the aquarium trade but often they do not do very well in captivity; juveniles are more highly prized than adults. ◆

Yellowspotted sawtail
Prionurus maculatus

FAMILY
Acanthuridae

TAXONOMY
Prionurus maculatus Ogilby, 1887, Port Jackson, New South Wales, Australia.

OTHER COMMON NAMES
German: Gelbfleken-Sägedoktor; Japanese: Nizadai.

PHYSICAL CHARACTERISTICS
Body is compressed and slightly elongated, with a protruding mouth and a snout with a dorsal profile that is slightly concave. there are nine spines and 24–26 soft rays in the dorsal fin, three spines and 23–25 soft rays in the anal fin, 17–18 soft rays in the pectoral fin, and one spine and five rays in the pelvic fin. the caudal fin is slightly emarginate to truncate in shape. as with other members of this genus, this species is distinguished by the presence of three peduncular plates, each having a lateral keel on either side of the caudal peduncle. the body coloration is bluish gray with several small yellow spots. the peduncular plates are black, and the keels are blue, usually with a white mark on the last plate. the caudal fin is gray with yellow spots and has a deep blue margin, as does the anal fin. juveniles have a series of narrow yellow bars that eventually, with age, become vertical rows of yellow spots. grows to about 17.3 in (44 cm) in length.

DISTRIBUTION
Western Pacific and restricted to the Southern Hemisphere, from southern Queensland on the Great Barrier Reef south to New South Wales and east to Lord Howe Island, Norfolk Island, and the Kermadec Islands. Waifs recruit seasonally to New Zealand during warmer summer months but probably do not reproduce successfully.

HABITAT
Tropical and warm temperate waters in protected areas of coral reefs, rocky reefs, and bays but also on outer coral and rocky reefs. Depth range is 6.6–98 ft (2–30 m).

BEHAVIOR
This species usually is found in aggregations.

FEEDING ECOLOGY AND DIET
Herbivorous. Feeds on benthic algae that grows mainly on rocks or coral substrates.

REPRODUCTIVE BIOLOGY
Probably pair-spawns but also may form spawning aggregations in which pair spawning occurs. Males probably change color pattern to attract a female from the aggregation, and the two touch their ventral surfaces together before the release of gametes, without an upward dash into the water column. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be taken incidentally as a food fish. ◆

Yellow tang
Zebrasoma flavescens

FAMILY
Acanthuridae

TAXONOMY
Zebrasoma flavescens Bennett, 1828, Hawaiian Islands.

OTHER COMMON NAMES
German: Gelber Segelflosser; Japanese: Kiirohagi.

PHYSICAL CHARACTERISTICS
Body is compressed and disc-like, with a concave head, a pronounced snout, and a protruding mouth. The dorsal fin is highly elevated and has four to five spines and 23–26 soft rays. The anal fin has three spines and 19–22 soft rays, and the pectoral fin has 14–16 soft rays. The body is a bright yellow, but the caudal spine sheath is white. Known to hybridize with *Z. scopas*. Grows to more than 7.9 in (20 cm) in length.

DISTRIBUTION
Tropical waters of the northern Pacific Ocean, from Minamitori-shima (Marcus Island) east to Wake Island, the Marshall Islands (uncommon), the Hawaiian Islands, and Johnston Island. Also in the Ogasawara, Ryukyu, and Mariana Islands. A waif was reported from Hong Kong, and other records, both in Polynesia and in the Indian Ocean, are probably xanthic morphs of *Z. scopas*.

HABITAT
Coral and rocky reefs, either exposed reef slopes to 265 ft (81 m) or in bays and lagoons as shallow as 3.3 ft (1 m).

BEHAVIOR
May be found in small groups or singly. Groups often move from point to point to browse on algae. Sometimes observed in mixed-species schools.

FEEDING ECOLOGY AND DIET
Herbivorous. Browses on filamentous algae on coral reefs.

REPRODUCTIVE BIOLOGY
This species has two mating systems. Single males may defend territories, court passing females, and engage in pair spawning in the water column. Alternatively, group spawning at spawning aggregation sites occurs. The spawning season is limited by the effects of seasonally cooler water temperatures at higher latitudes. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN but subject to overfishing, particularly in parts of the Hawaiian Islands, for the aquarium trade.

SIGNIFICANCE TO HUMANS
An important species in the aquarium trade and the number one exported species from the Hawaiian Islands. ◆

Longfin spadefish
Platax teira

FAMILY
Ephippidae

TAXONOMY
Platax teira Forsskal, 1775, Luhaiya, Yemen, Red Sea.

OTHER COMMON NAMES
English: Teira batfish; French: Poisson lune; German: Langflossen-Fledermausfisch; Japanese: Mikazuki-tsubame-uo.

PHYSICAL CHARACTERISTICS
Body is deep and highly compressed. The dorsal fin is continuous, and the anal, dorsal, and pelvic fins are greatly elevated. Scales are ctenoid and small. The mouth is terminal, with tricuspid teeth. Juveniles also have deep bodies and elevated anal, dorsal, and pelvic fins (the latter extremely long), with the dorsal and anal fins extending backward beyond the caudal fin. These fins are reduced in size somewhat with age (i.e. the fins do not grow with age relative to the rest of the body). Larvae have a deep or moderately deep body and a relatively compressed caudal fin; the head and trunk are combined into a broad, ball-like structure that eventually deepens with growth. There are no scales present on the body of the larvae at settlement. Settlement refers to the transformation of a pelagic-dwelling larva to a Reef-dwelling post-larva or juvenile. Grows to more than 17.7 in (45 cm) in length.

DISTRIBUTION
Tropical and subtropical waters from the Red Sea and Indian Ocean east to Fiji, north to southern Japan, and south to Australia's Great Barrier Reef and Lord Howe Island.

HABITAT
Coral and rocky reefs, usually drop-offs, deep lagoons, and pinnacles along the outer reef to a depth of at least 66 ft (20 m). Juveniles usually are found in protected areas of shallow reefs and bays.

BEHAVIOR
Occurs singly or in small aggregations as adults and juveniles. Juveniles often mimic floating leaves in shallow waters.

FEEDING ECOLOGY AND DIET
Omnivorous, feeding on a variety of small benthic invertebrates and algae.

REPRODUCTIVE BIOLOGY
Probably pair-spawns within aggregations or smaller groups. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade. ◆

Louvar
Luvarus imperialis

FAMILY
Luvaridae

TAXONOMY
Luvarus imperialis Rafinesque, 1810, Sicily, Italy.

OTHER COMMON NAMES
Japanese: Amashiira.

PHYSICAL CHARACTERISTICS
Fusiform body, which is compressed slightly and streamlined. Pelvic fins are absent. The head is blunt, with a projecting forehead, and there is a groove above the eye. Opercular spines are flattened. Scales are dentroid and minute. The caudal peduncle has small accessory keels that flank the large caudal keel. The mouth is small and slightly protrusible. Metamorphosis from larvae to adults involves considerable change. Numerous juvenile characters are absent in adults. For example, juveniles possess jaw teeth, fin spines, and a rudimentary locking mechanism. Grows to 78.7 in (200 cm) in length.

DISTRIBUTION
Tropical, subtropical, and temperate waters of the Atlantic (including the Mediterranean Sea), Indian, and Pacific Oceans.

HABITAT
Epipelagic, from the surface to relatively deeper waters.

BEHAVIOR
Poorly known. This species generally is solitary in the open ocean but probably aggregates for courtship and spawning.

FEEDING ECOLOGY AND DIET
Feeds on gelatinous mesoplankton, primarily jellyfishes and ctenophores.

REPRODUCTIVE BIOLOGY
Not well known. Spawning commences in late spring and runs throughout the summer months. Species is reportedly quite fecund; one female examined had an estimated 47.5 million eggs. Pelagic spawning with pelagic larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be taken incidentally in commercial fisheries. ◆

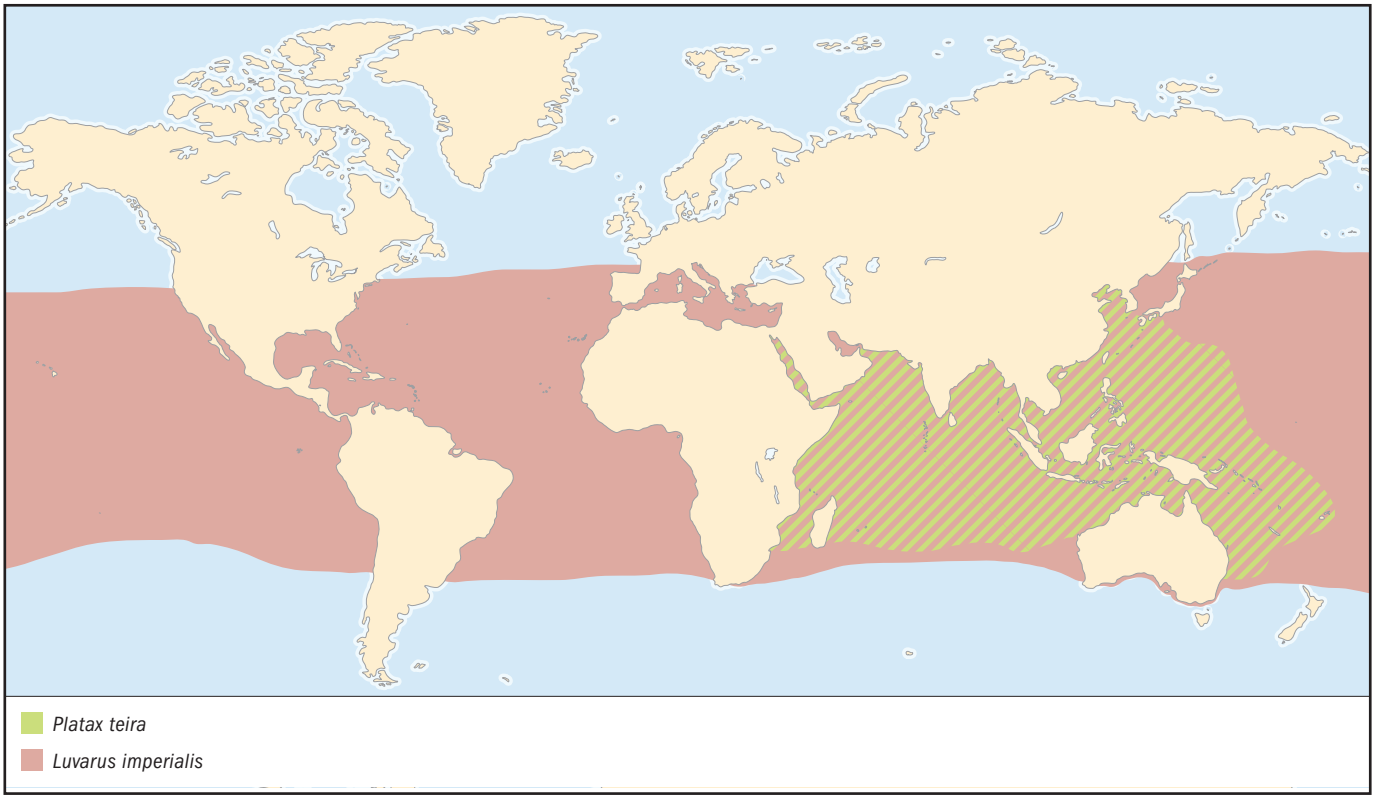
Spotted scat
Scatophagus argus

FAMILY
Scatophagidae

TAXONOMY
Scatophagus argus Linnaeus, 1758, India. No type specimens are known.

OTHER COMMON NAMES
Japanese: Kurohoshimanjûdai.

PHYSICAL CHARACTERISTICS
Body is deep and compressed, with a deeply notched dorsal fin, a pronounced forehead, and a nonprotrusible mouth. There



are 10–11 spines and 16–18 soft rays in the dorsal fin, four spines and 13–15 soft rays in the anal fin, and 16 branched rays in the caudal fin. The spines are sharp and are reported to be venomous. The pelvic fins are attached by an axillary process. Body color is silvery green to orange, with numerous small dark spots on the flank and on the base of the dorsal, caudal, and anal fins. Larvae have a specialized stage similar to the tholichthys of larval butterflyfishes (Chaetodontidae). Grows to about 15 in (38 cm) in length.

DISTRIBUTION
Indo-West Pacific region from Kuwait east to Vanuatu and New Caledonia, south to Australia, north to southern Japan, and east to Pohnpei (Micronesia). Also reported from Samoa and the Society Islands.

HABITAT
Inshore marine, brackish, and freshwaters, usually in turbid estuaries, harbors, back bays, mangrove stands, and reefs.

BEHAVIOR
Not well known. Occurs in small groups or aggregations.

FEEDING ECOLOGY AND DIET
Omnivorous, feeding on small invertebrates, including worms, crustaceans, and insects, and on benthic algae. Genus name was coined from observation of members of this genus feeding on feces and sewage discharged by ships into harbors and bays.

REPRODUCTIVE BIOLOGY
Not well known, except from aquarium observations. Reported to spawn demersal eggs and engage in parental care, traits inconsistent with most other species in this suborder, though somewhat similar to the Siganidae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade for display in marine and freshwater aquaria. Also taken for subsistence or artisanal food fisheries and has been grown by commercial aquaculture for the live reef food fish trade. ◆

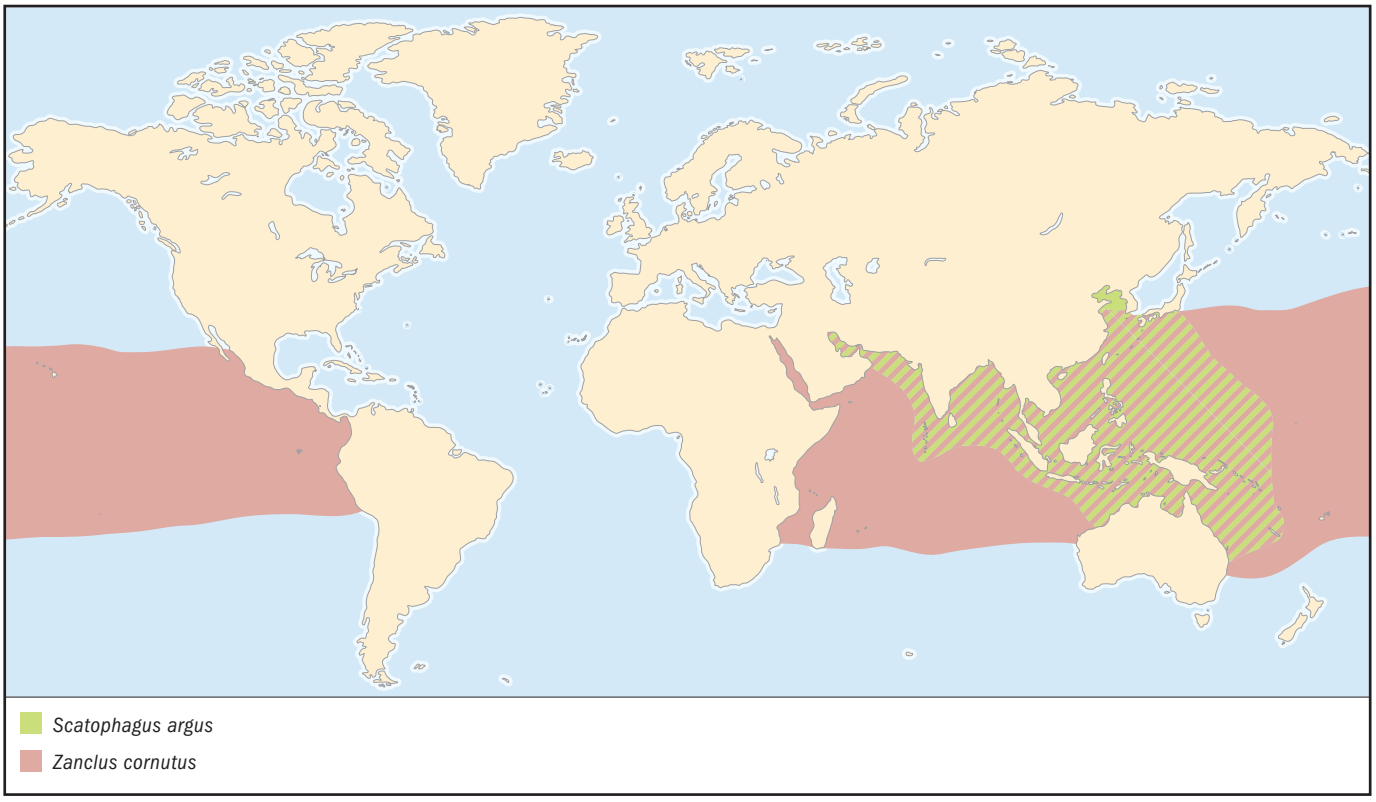
Foxface rabbitfish
Siganus vulpinus

FAMILY
Siganidae

TAXONOMY
Siganus vulpinus Schlegel and Muller, 1844, Ternate Island, Moluccas Islands, Indonesia.

OTHER COMMON NAMES
English: Foxface; German: Gelbes Dachsgesicht; Japanese: Hifuki-aigo.

PHYSICAL CHARACTERISTICS
Body is compressed and elongate, with minute cycloid scales on the trunk. There is a single dorsal fin with 13 spines and 10 soft rays. The pelvic fins are positioned at the thorax. The pectoral fin usually has 16 rays. Fin spines are stout and venomous. The snout is long and tubelike. Body color is predominately yellow, with a chocolate-brown forehead and snout and white spotted with brown on the preopercle and opercle and on the flank directly behind the gills. The thorax



is chocolate brown, and this color extends down to the first two pelvic fin spines. The dorsal, anal, and caudal fins are yellow; the pectoral and pelvic fins are white. There is some variation between individuals. Grows to at least 9.8 in (25 cm) in length.

DISTRIBUTION
Indo-West Pacific region from Sumatra east to the Marshall Islands and south to the Great Barrier Reef and New Caledonia.

HABITAT
Seaward reefs and outer slopes, lagoons, and deeper reef flats to a depth of 98 ft (30 m). Prefers lush coral growth. Juveniles and subadults take refuge in staghorn corals.

BEHAVIOR
Larvae, juveniles, and subadults occur in large schools. Pair formation, possibly monogamous, occurs when the species reaches 3.9 in (10 cm) in length. Pairs patrol a restricted home range and at times may defend a territory.

FEEDING ECOLOGY AND DIET
A browsing herbivore that feeds upon benthic algae found on the substrate or upon dead corals.

REPRODUCTIVE BIOLOGY
Descriptions of reproductive biology of this and some other siganid species are based largely upon observations of captive individuals augmented by some field observations. This species spawns in pairs at dusk or dawn in relation to moon phase. Eggs are spherical and adhesive, measuring 0.02–0.025 in (0.55–0.66 mm), and are scattered on substrate (some siganid species have pelagic eggs, however). Larvae hatch out and measure about 0.08 in (2 mm) in length. They have a large yolk, an unformed mouth, a straight gut, unpigmented eyes, and a pattern of body pigmentation that is relatively stable with growth. Body shape is elongate, but this becomes deeper and laterally compressed with growth. Fin development begins before the yolk is absorbed and spines appear at about 0.11 in (3 mm) in length. Fin rays form at about 0.24 in (6 mm), but scales do not form until larval settlement. The larvae have the following specializations for pelagic life: long dorsal and pelvic fins that form early in development, fin spines that are serrate in shape, and the formation of spines upon the head.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
May be taken by subsistence and artisanal fisheries for food. Also collected for the aquarium trade. ◆

Moorish idol

Zanclus cornutus

FAMILY
Zanclidae

TAXONOMY
Zanclus cornutus Linnaeus, 1758, Indian seas. No type specimens are known.

OTHER COMMON NAMES
French: Cocher jaune; German: Halterfisch; Japanese: Tsunodashi.

PHYSICAL CHARACTERISTICS
Superficially, this species resembles the butterflyfishes (Chaetodontidae). The body is strongly compressed and disc-like, the snout is tubular, and the mouth is small, with many elongated, bristle-like teeth. The third dorsal spine is long and whiplike (the "streamer"). Coloring consists primarily of three vertical bands of white and yellow in alternation with two bands of black. The caudal fin is also black and fringed with white or yellowish white. A small patch of yellow and a horizontal band of white occur on the snout. Larvae are distinguished by a third spine that is elongate and more than twice the length of the larva's body, which develops into the "streamer" of adults. Also has a spine positioned prominently above the corner of the mouth. Body size is large, up to about 3 in (7.5 cm) in length, at metamorphosis from postlarvae to juveniles. Adults grow to at least 5.9 in (15 cm) in length.

DISTRIBUTION
Tropical and subtropical waters of the Indo-Pacific region from East Africa in the Indian Ocean east to the Hawaiian Islands, Rapa Island, and Ducie Atoll in the east-central Pacific and in southern Gulf of California south to Peru in the eastern Pacific. In the western Pacific, north to southern Japan, south to Australia and Lord Howe Island, and throughout Micronesia, Polynesia, and Melanesia.

HABITAT
Clear seaward coral and rocky reefs, reef flats, and turbid inner lagoons. Depth range from less than 9.8 ft (3 m) to more than 591 ft (180 m).

BEHAVIOR
Found singly, in pairs, or in small groups of three or more. Occasionally, large aggregations in excess of 150 fishes are seen; such aggregations may be for spawning.

FEEDING ECOLOGY AND DIET
Feeds on benthic encrusting invertebrates, especially sponges, that it plucks from the substrate.

REPRODUCTIVE BIOLOGY
Still poorly known. Pair-spawns at dusk on seaward reefs within small groups or, possibly, in larger aggregations. Eggs and larvae are pelagic, and larval life can be relatively long, thus potentially explaining their broad pattern of distribution as adults.

CONSERVATION STATUS
Not listed by the IUCN. Aquarium trade is restricted in Germany.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade but does not do well in most aquaria. Also taken in subsistence food fisheries. ◆

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

Terry J. Donaldson, PhD

Scombroidei

(Barracudas, tunas, marlins, and relatives)

Class Actinopterygeii
Order Perciformes
Suborder Scomboidei
Number of families 6

Photo: A marlin leaps out of the water. (Photo by Scott Kerrigan/Corbis. Reproduced by permission.)

Evolution and systematics

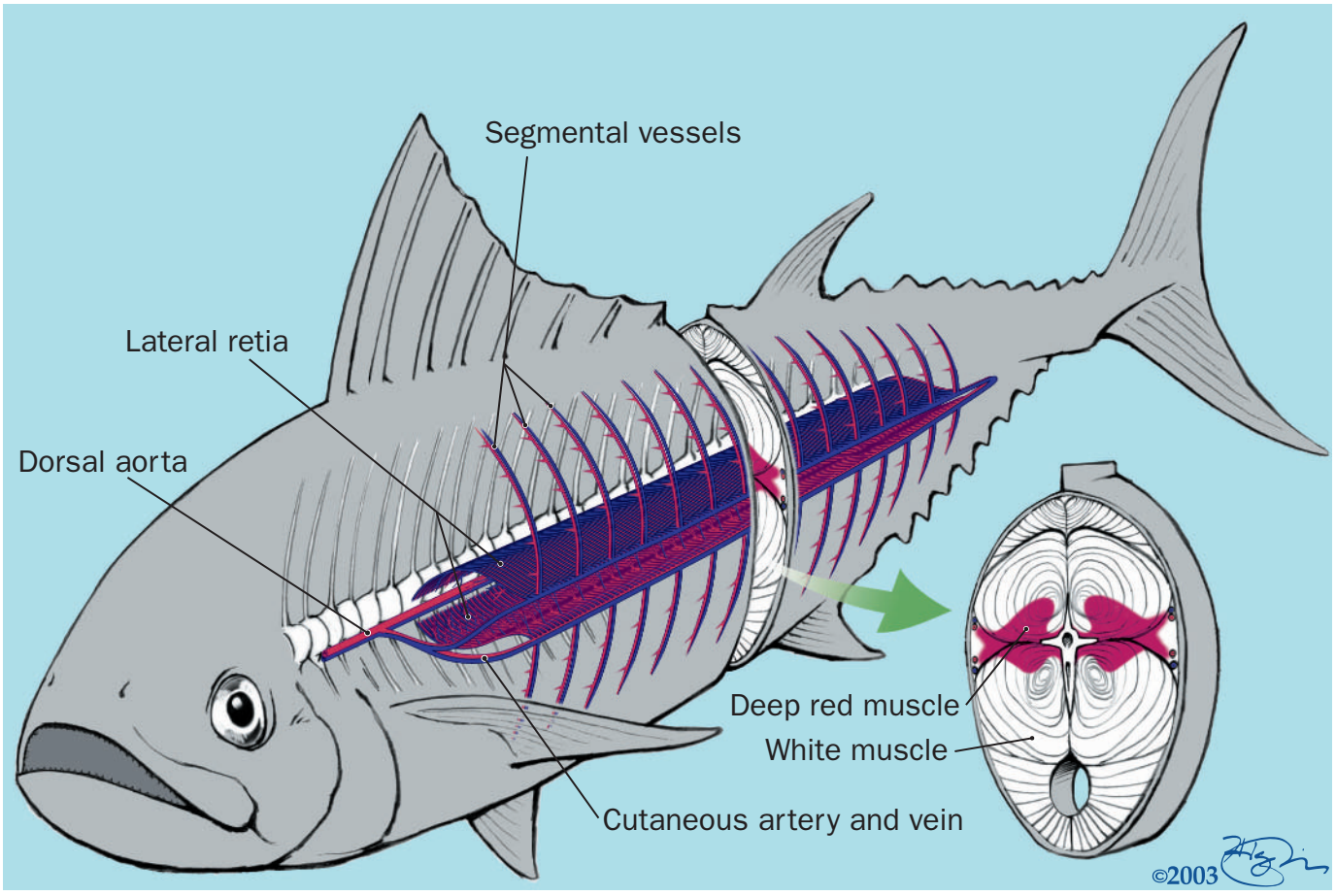
The first modern definition of the scombroid fishes as a suborder was by Regan in 1909. He clearly separated scombroids from percoid families, such as the jacks (Carangidae) and dolphinfishes (Coryphaenidae). Regan recognized four divisions within the Scombroidei: Trichiuriformes (Gempylidae and Trichiuridae), Scombriformes (Scombridae), Luvariformes (Luvaridae), and Xiphiiformes (Xiphiidae, Istiophoridae, and three fossil families). The suborder was redefined by Collette et al. (1984), and the Luvaridae were shown to be a highly specialized oceanic member of the typically reef-associated surgeonfishes (Acanthuroidei) by Tyler et al. (1989). Collette et al. (1984) included the Scombrolabricidae in the Scombroidei as its most primitive member. An alternative definition of the Scombroidei proposed by Johnson in 1986 excludes the Scombrolabracoidei but includes the barracudas (Sphyraenidae) as the most primitive member of the Scombroidei.

The 6 families are Sphyraenidae (1 genus, 20 species), Trichiuridae (9 genera, 32 species), Gempylidae (16 genera, 23 species), Scombridae (15 genera, 53 species), Xiphiidae (1 genus, 1 species), and Istiophoridae (3 genera, 9 species).

A school of barracuda in defensive behavior surround a diver in the Bismarck Sea near Papua New Guinea. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

Physical characteristics

Perciform fishes with epiotic bones of the skull separated from each other by the supraoccipital bone; gill membranes



Tuna can regulate their temperature through blood flow. Increased blood flow in vessels near the skin allows heat to dissipate into the environment, cooling the fish. (Illustration by Jonathan Higgins)

free from the isthmus; premaxillae beak like, upper jaw not protrusile, predorsal bones lost (except for a small one in *Ruvettus*, *Thyrsites*, and *Tongaichthys*, and three well-developed ones in *Gasterochisma*); second epibranchial bone of pharyngeal arch extending over top of the third infrapharyngobranchial bone (except in *Gasterochisma*); 24 or more vertebrae; interorbital commissure of the supraorbital lateral line canals incomplete or absent

Distribution

These fishes are found in marine and estuarine waters of tropical and temperate oceans of the world. One species of Spanish mackerel moves long distances up the Mekong River.

Habitat

Most scombroid fishes are epipelagic; some are mesopelagic.

Behavior

Some scombroids (such as mackerels) form very large schools while others (such as wahoo and snake mackerels) are essentially solitary.

Feeding ecology and diet

Most scombroids are active predators, feeding on a wide variety of fishes, squids, and crustaceans, but some (such as the mackerels) filter small planktonic organisms out of the water with their long gillrakers.

Smaller species of scombroids, such as mackerels, fall prey to all larger predacious sea animals. Whales, porpoises, sharks, tunas, bonito, bluefish, and striped bass take a heavy toll. Cod often eat small mackerel; squids destroy great numbers of young fish; and seabirds of various kinds follow and prey upon the schools when these are at the surface.

Medium-sized scombroids such as bonitos and skipjack are preyed upon by tunas, billfishes, and sharks. Predators of large tunas like the bluefin include killer whales and such sharks as the white shark and the mako shark. Large billfishes are so active and powerful that they have few enemies but are preyed upon by killer and sperm whales and mako sharks.

Reproductive biology

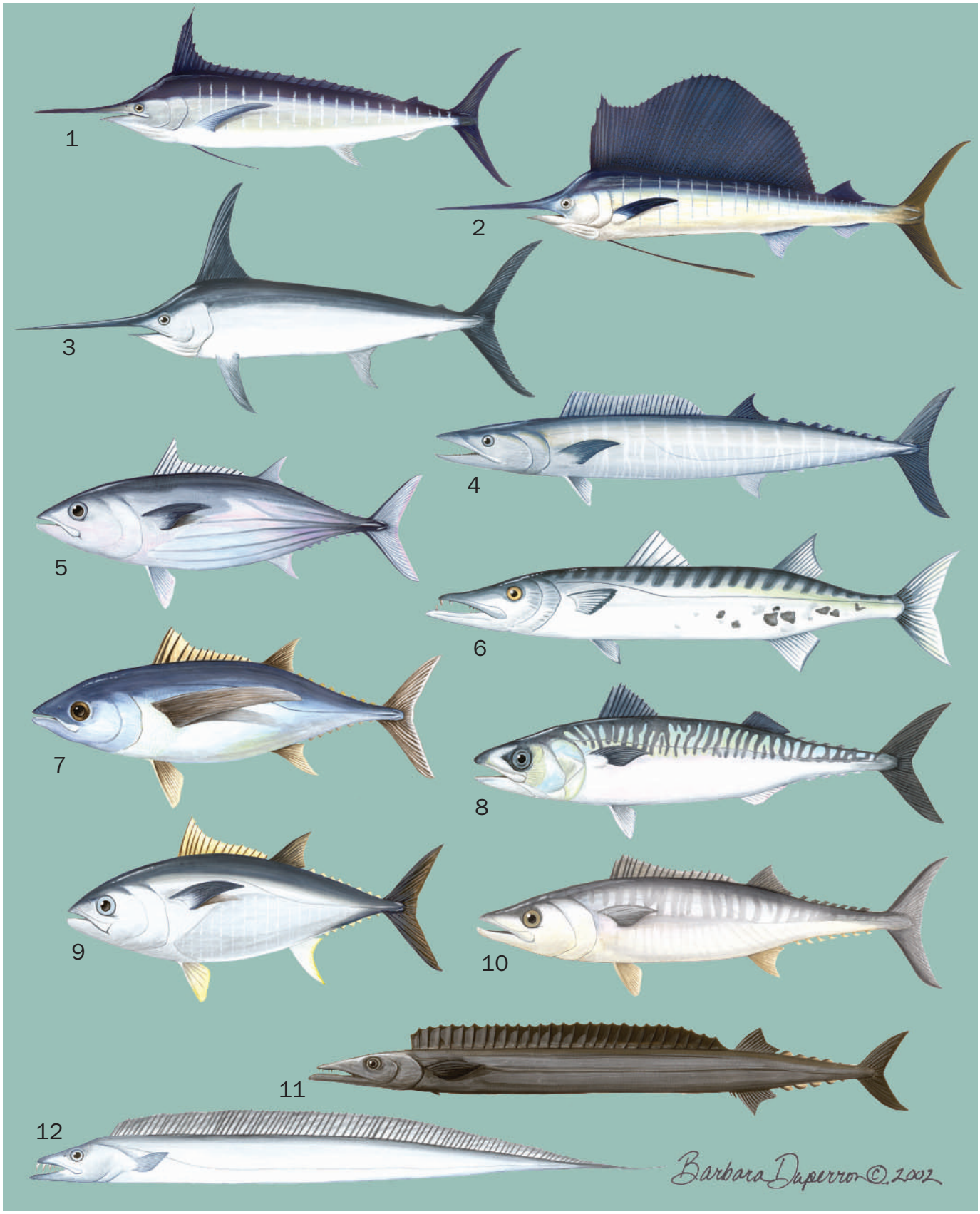
Scombroids are dioecious (separate sexes) and most display little or no sexual dimorphism in structure or color pattern. Batch spawning of most species takes place in tropical and subtropical waters, frequently inshore. The eggs are pelagic and hatch into planktonic larvae.

Conservation status

Populations of three species, swordfish (*Xiphias gladius*), Atlantic bluefin tuna (*Thunnus thynnus*), and Atlantic albacore (*Thunnus alalunga*), have been greatly reduced by fishing. All three are listed by the IUCN as Data Deficient. In addition, the IUCN categorizes the Monterrey Spanish mackerel (*Scomberomorus concolor*) as Endangered, the southern bluefin tuna (*Thunnus maccoyii*) as Critically Endangered, and the bigeye tuna (*Thunnus obesus*) as Vulnerable.

Significance to humans

Many species of scombroid fishes are of great importance as food fishes—mackerel, Spanish mackerel, bonito, and tuna—and as sport fishes—Spanish mackerel, tuna, swordfish, and marlin.



1. Blue marlin (*Makaira nigricans*); 2. Sailfish (*Istiophorus platypterus*); 3. Swordfish (*Xiphias gladius*); 4. Wahoo (*Acanthocybium solandri*); 5. Skipjack tuna (*Katsuwonus pelamis*); 6. Great barracuda (*Sphyraena barracuda*); 7. Albacore (*Thunnus alalunga*); 8. Atlantic mackerel (*Scomber scombrus*); 9. Atlantic bluefin tuna (*Thunnus thynnus*); 10. King mackerel (*Scomberomorus cavalla*); 11. Snake mackerel (*Gempylus serpens*); 12. Largehead hairtail (*Trichiurus lepturus*). (Illustration by Barbara Duperron)

Species accounts

Snake mackerel
Gempylus serpens

FAMILY
Gempylidae

TAXONOMY
Gempylus serpens Cuvier, 1829, Tropic of Cancer.

OTHER COMMON NAMES
French: Escolier serpent; Spanish: Escolar de canal.

PHYSICAL CHARACTERISTICS
Maximum length approximately 40 in (1 m), commonly to 24 in (60 cm). Body greatly elongate and strongly compressed. Tips of upper and lower jaws with cartilaginous processes. Three immovable and zero to three movable fangs anteriorly in upper jaw. First dorsal fin long with 26–32 spines, second dorsal fin with 11–14 soft rays followed by five or six finlets. Caudal fin well developed. Scales absent except on posterior part of body.

DISTRIBUTION
Worldwide in tropical and subtropical seas; adults also caught in temperate waters.

HABITAT
Strictly oceanic, epipelagic and mesopelagic from the surface to depths of 656 ft (200 m).

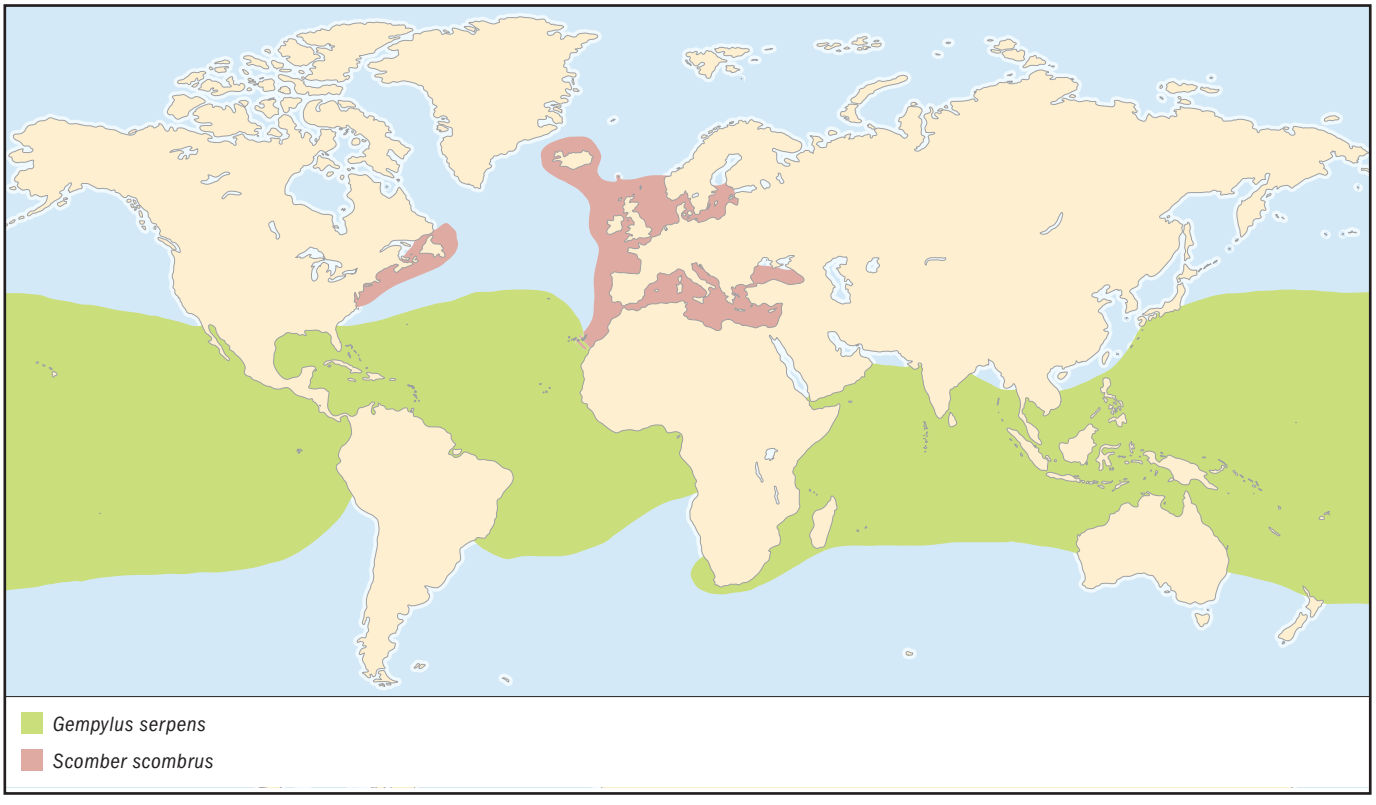
BEHAVIOR
Usually solitary. Adults migrate to the surface at night; larvae and juveniles stay near the surface only during the day.

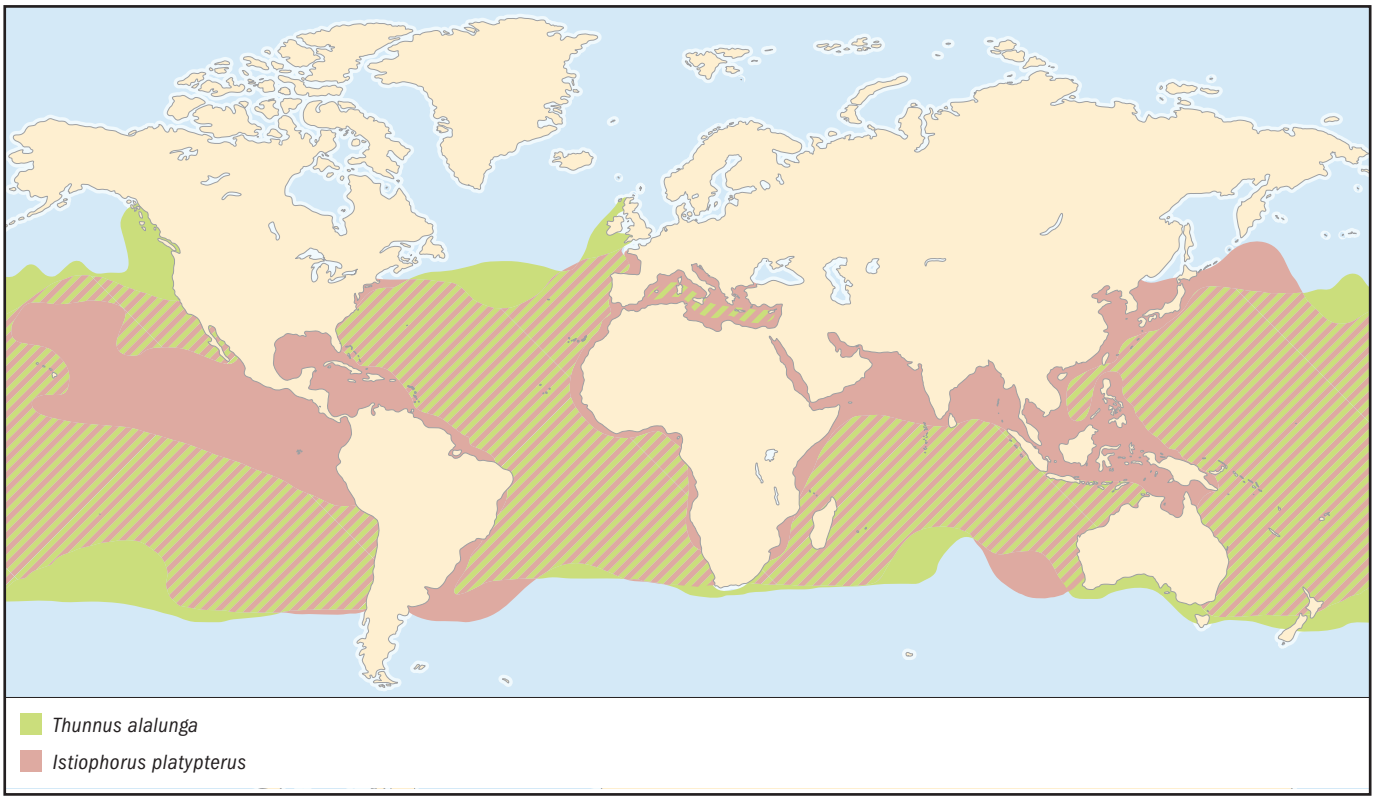
FEEDING ECOLOGY AND DIET
Feed on fishes such as lanternfishes, flyingfishes, sauries, and scombrids and on squids and crustaceans.

REPRODUCTIVE BIOLOGY
Males mature at approximately 17 in (43 cm) standard length, females at 20 in (50 cm). Spawn in tropical waters throughout the year. Fecundity is estimated at 300,000 to one million eggs.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
There is no directed fishery for snake mackerel, but it sometimes appears as bycatch in the tuna long-line fishery. ◆





Sailfish

Istiophorus platypterus

FAMILY
Istiophoridae

TAXONOMY
Istiophorus platypterus (Shaw, 1792), Indian Ocean. Some authors, such as Nakamura (1985), differentiate the Atlantic sailfish, *I. albicans* (Latreille, 1804), as a separate species.

OTHER COMMON NAMES
French: Voilier; Spanish: Pez vela.

PHYSICAL CHARACTERISTICS
Sailfishes reach a maximum size of approximately 11 ft (3.5 m) total length and 220 lb (100 kg). Body fairly compressed. Two dorsal and two anal fins, the first dorsal fin sail-like and remarkably higher than greatest body depth, with 42–49 rays. Second dorsal fin with six or seven rays, slightly posterior to second anal fin which also has six or seven rays. Pectoral fins moderate, 18–20 rays. Pelvic fins extremely long, almost reaching the anus, depressable into a groove, with one spine and several rays tightly fused together. Jaws and palatine bones with small, file-like teeth. Gill rakers absent. Left and right branchiostegal membranes broadly united. Vertebrae, 24. Swim bladder made up of many small bubble-shaped chambers.

DISTRIBUTION
Most researchers consider the sailfish to be a single pantropical species occurring in all three major oceans.

HABITAT
An epipelagic and oceanic species, usually found above the thermocline. Sailfishes have a strong tendency to approach continental coasts, islands, and reefs.

BEHAVIOR
Sailfishes occasionally form schools or smaller groups of 3–30 individuals, but more often occur in loose aggregations over a wide area.

FEEDING ECOLOGY AND DIET
Feeding behavior has been observed by fishermen: One or several sailfish locate a school of prey fish (such as sardines, anchovies, mackerel, or jack mackerel) and pursue the school at half speed with their fins half-folded back into the grooves. They then drive at the prey at full speed with fins completely folded back and make sharp turns with fins expanded to confront part of the school and strike the prey with their bills. They feed on the killed or stunned fish, usually head first as well as on a variety of fishes, crustaceans, and squid.

REPRODUCTIVE BIOLOGY
Spawning occurs with males and females swimming in pairs or with two or three males chasing one female. Sailfishes spawn throughout the year in tropical and subtropical waters with peak spawning in local summer seasons. Ripe ovarian eggs are approximately 0.03 in (0.85 mm) in diameter and have a single oil globule. Eggs shed from a captured female averaged 0.05 in (1.30 mm) in diameter.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sailfishes are often taken as bycatch by the commercial surface tuna long liners. United Nations Food and Agriculture Organization (FAO) catch statistics for 1991–2000 show catches of 11.1–23.7 thousand tons (10.1–21.5 thousand metric tons) per year by 42 countries. Sailfishes are primarily important as a sportsfish taken by trolling at the surface. The all-tackle gamefish record is a 221-lb (100.2-kg) fish taken off Santa Cruz Island, Ecuador. ◆

Blue marlin

Makaira nigricans

FAMILY
Istiophoridae

TAXONOMY
Makaira nigricans Lacepede, 1802, Bay of Biscay. Some authors, such as Nakamura (1985), differentiate the Indo-Pacific blue marlin, *M. mazara* (Jordan and Snyder, 1901), as a separate species.

OTHER COMMON NAMES
French: Makaire bleu; Spanish: Aguja azul.

PHYSICAL CHARACTERISTICS
Blue marlin reach approximately 16 ft (5 m) in total length and weigh more than 1,984 lb (900 kg). Body not very compressed, nape highly elevated, body deepest at level of pectoral fins. Two dorsal and two anal fins. First dorsal fin with 39–43 rays; height of anterior lobe less than greatest body depth, not sail-like. Second dorsal fin with six or seven rays, slightly posterior to second anal fin. Pectoral fins with 20–23 rays, depressible against sides of the body. Pelvic fins shorter than pectoral fins with one spine and two rays. Lateral line looped. Body covered with densely imbedded scales, each with one or two long, acute spines. Left and right branchiostegal membranes broadly united. Vertebrae, 24. Swim bladder made up of many small bubble-shaped chambers. Body blue dorsally, silvery white ventrally, first dorsal fin membrane blue-black, unspotted; body has approximately 15 obscure vertical light bars.

DISTRIBUTION
Most researchers consider the blue marlin to be a single pantropical species occurring in all three major oceans. Blue marlin are the most tropical of the billfishes, chiefly distributed in equatorial areas.

HABITAT
Epipelagic zone of oceans, usually waters with surface temperatures of 71.6–87.8°F (22–31°C).

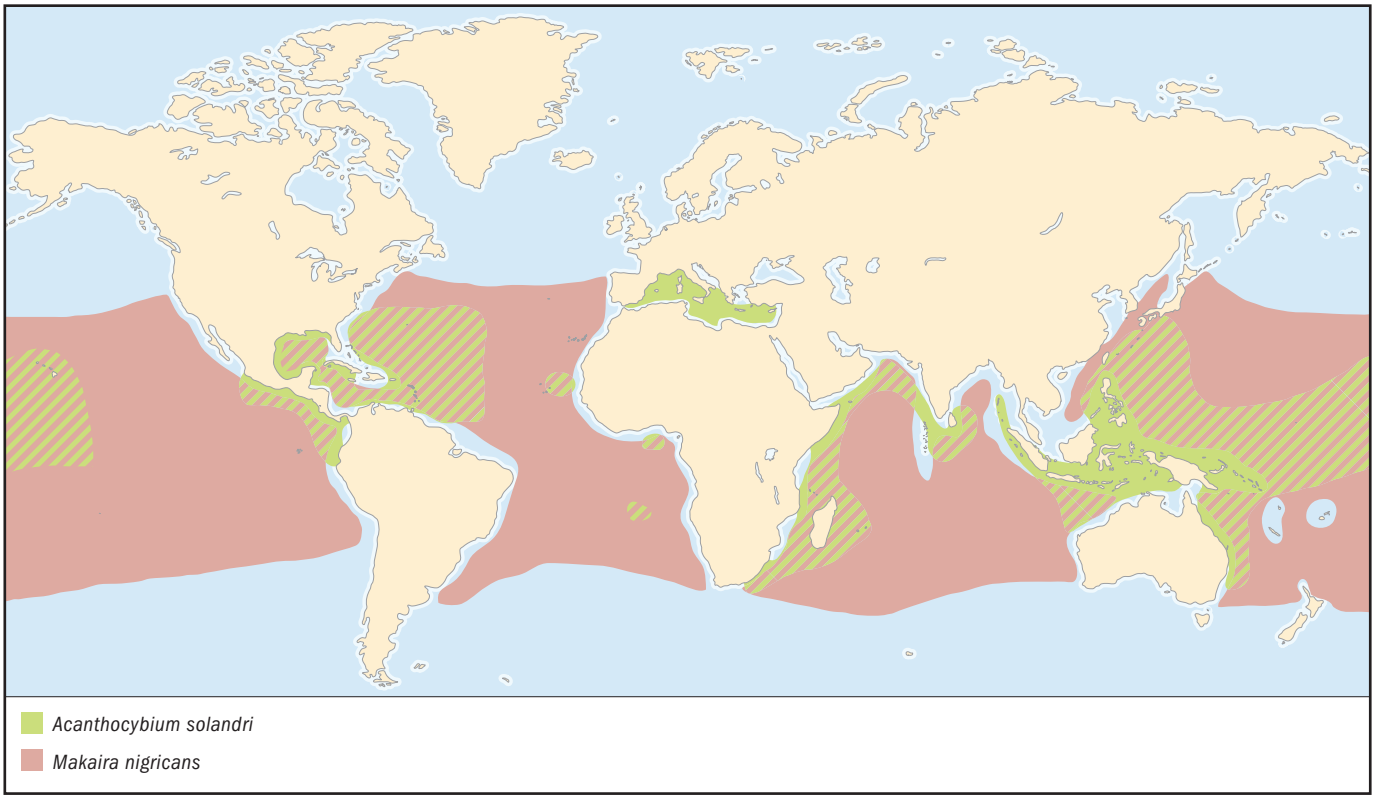
BEHAVIOR
Observations suggest that marlins use their bills to stun their prey.

FEEDING ECOLOGY AND DIET
Feed mostly in near-surface waters but sometimes make trips to relatively deep waters for feeding. Prey includes dolphinfishes, tuna-like fishes, particularly frigate tunas, and squids.

REPRODUCTIVE BIOLOGY
Little is known about spawning grounds or seasons. The eggs are very small, approximately 0.04 in (1 mm) in diameter, and pelagic, hatching into planktonic larvae.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Being excellent foodfishes, all species of marlin are of some importance to fisheries, particularly in Japan. They are mostly caught on long lines incidental to the target tuna species. FAO catch statistics for 1991–2000 show catches of 26.7–37.3 thousand tons (24.2–33.8 thousand metric tons) per year by 34 countries. Blue marlin are especially important to sportfishermen and are much sought after off Cuba and on the Bahamas side of the Straits of Florida. The all-tackle gamefish record is a 1,402-lb (636-kg) fish taken off Vitória, Brazil. ◆



Wahoo
Acanthocybium solandri

FAMILY
Scombridae

TAXONOMY
Acanthocybium solandri (Cuvier, 1832), type locality unknown.

OTHER COMMON NAMES
French: Thazard-bâtard; Spanish: Peto.

PHYSICAL CHARACTERISTICS
Maximum size 83 in (210 cm) fork length weighing 183 lb (83 kg) or more. Body very elongate, fusiform, and only slightly compressed. Mouth large with strong, triangular, compressed, and finely serrate teeth closely set in a single series. Snout approximately as long as rest of head. Gill rakers absent. Two dorsal fins, the first consisting of 23–27 spines, the second with 12–16 rays followed by eight or nine finlets. Anal fin of 12–14 rays followed by nine finlets. Body covered with small scales. Swim bladder present. Vertebrae, 62–64. Back iridescent bluish green, sides silvery with 24–30 cobalt-blue vertical bars.

DISTRIBUTION
Tropical and subtropical waters of the Atlantic, Pacific, and Indian oceans including the Caribbean and Mediterranean seas.

HABITAT
Epipelagic zone ocean.

BEHAVIOR
Frequently solitary or forming small, loose aggregations rather than compact schools.

FEEDING ECOLOGY AND DIET
Piscivorous, preying on pelagic fishes such as scombrids, porcupinefishes, flyingfishes, herrings, scads, and lanternfishes and on squids.

REPRODUCTIVE BIOLOGY
Spawning seems to extend over a long period. Fish in different maturity stages are frequently caught at the same time. Fecundity is believed to be quite high; 6 million eggs were estimated for a 52-in (131-cm) female.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
There do not appear to be any organized fisheries for wahoo, but it is greatly appreciated when caught. FAO catch statistics for 1991–2000 show catches of 2,121–3,460 tons (1,924–3,139 metric tons) per year by 30 countries. In many areas (Caribbean, Hawaii, Great Barrier Reef), wahoo is more important as a gamefish taken on light to heavy tackle through surface trolling with spoons, feather lures, or strip bait. The all-tackle gamefish record is a 159-lb (71.9-kg) fish taken off Baja California. ◆

Skipjack tuna
Katsuwonus pelamis

FAMILY
Scombridae

TAXONOMY
Katsuwonus pelamis (Linnaeus, 1758), "pelagic, between the tropics."

OTHER COMMON NAMES
French: Bonite à ventre rayé; Spanish: Listado.

PHYSICAL CHARACTERISTICS
Maximum fork length approximately 43 in (108 cm) corresponding to a weight of 72–76 lb (32.5–34.5 kg), commonly to 31 in (80 cm) and 18–22 lb (8–10 kg). Body fusiform, elongate, and rounded. Two dorsal fins separated by a narrow interspace, the first with 14–16 spines, the second dorsal and anal fins followed by seven to nine finlets. Pectoral fins short, with 26 or 27 rays. Body naked except for anterior corselet and lateral line. Caudal peduncle very slender with a strong lateral keel between two smaller keels. Swim bladder absent. Gill rakers numerous, 53–63 on first gill arch. Back dark purplish blue, lower sides and belly silvery, with four to six very conspicuous longitudinal dark bands.

DISTRIBUTION
Cosmopolitan in tropical and warm-temperate seas but absent from the Black Sea.

HABITAT
An epipelagic oceanic species with adults distributed within the 59°F (15°C) isotherm. Aggregations of this species tend to be associated with convergences, boundaries between cold and warm water masses. Depth distribution ranges from the surface to about 853 ft (260 m) during the day.

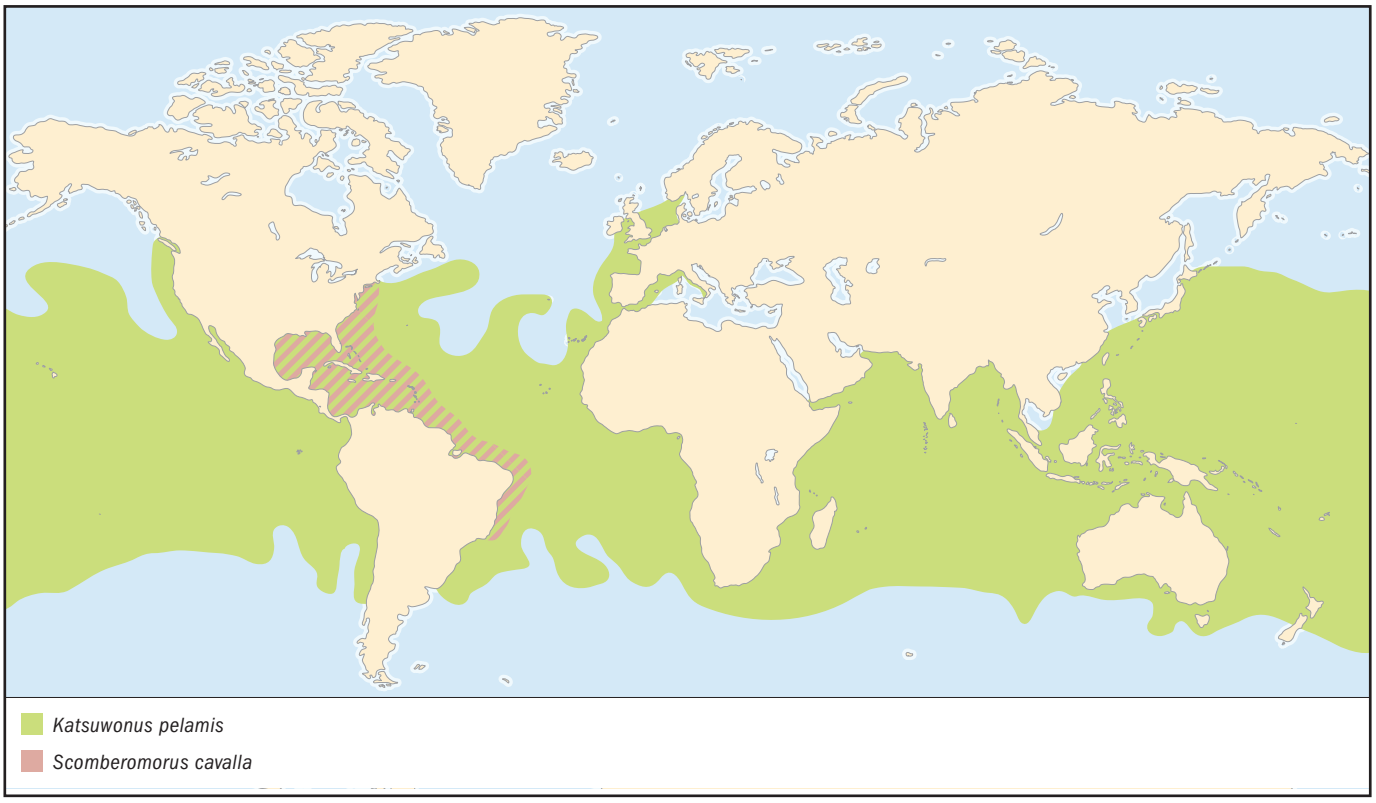
BEHAVIOR
Skipjack show a strong tendency to school in surface waters. Schools are associated with birds, drifting objects, sharks, whales, and other tuna species.

FEEDING ECOLOGY AND DIET
Skipjack are opportunistic feeders preying on any forage available. Feeding activity peaks in early morning and late afternoon. Food items include fishes, crustaceans, and mollusks.

REPRODUCTIVE BIOLOGY
Skipjack spawn in batches throughout the year in equatorial waters and from spring to early fall in subtropical waters. The spawning season becomes shorter as distance from the equator increases. Fecundity increases with size but is highly variable. The number of eggs per season in females 16–24 in (41–87 cm) fork length ranges from 80,000 to two million.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Skipjack make up approximately 40% of the world's total tuna catch and have come to replace yellowfin as the dominant commercial species of tuna. Catches of skipjack were reported to FAO by 94 countries for 1991–2000, 1,584–2,191 thousand tons (1,437–1,988 thousand metric tons) per year. The highest catches reported for 2000 were by Japan, 376 thousand tons (341 thousand metric tons), and Indonesia, 298 thousand tons (270 thousand metric tons). Skipjack are taken at the surface, mostly with purse seines and pole-and-line gear, occasionally with long lines. They are marketed fresh, frozen, and canned (as light-meat tuna). They are also a game fish, the all-tackle gamefish record is a 45-lb (20.5-kg) fish caught on Flathead Bank, Baja California. ◆



Atlantic mackerel

Scomber scombrus

FAMILY
Scombridae

TAXONOMY
Scomber scombrus Linnaeus, 1758, Atlantic Ocean.

OTHER COMMON NAMES
French: Maquereau commun; Spanish: Caballa del Atlantico.

PHYSICAL CHARACTERISTICS
Maximum fork length is 22 in (56 cm), commonly to 19 in (30 cm). Body fusiform, tapering rearward to a very slim caudal peduncle and anteriorly to a pointed snout. Eyes large with so-called adipose eyelids covering front and hind margins of the eye except for a slit over the pupil. Mouth large, filled with small, sharp, conical teeth in upper and lower jaws. Gill rakers, 30–36 on lower limb of first gill arch. Two widely separated dorsal fins, the first with 11–13 spines, the second with 11 or 12 rays. Both second dorsal and anal fins followed by five finlets. Entire body covered with small scales. Swim bladder usually absent. Vertebrae, 31. Upper surface dark steely to greenish blue. Body barred with 23–33 dark transverse bands; belly unmarked.

DISTRIBUTION
North Atlantic Ocean, including the Baltic, Mediterranean, and Black seas. Replaced by other species of *Scomber* in other oceans.

HABITAT
An epipelagic and mesodemersal species, most abundant in cold and temperate shelf areas.

BEHAVIOR
Mackerel are swift-moving, swimming with very short sidewise movements of the rear part of the body and the powerful caudal fin. They need so much oxygen that they must swim constantly to bring sufficient water across their gill filaments. Mackerel gather in dense schools of fish that are approximately the same size and age. They overwinter in moderately deep water along the continental shelf and move inshore and northward in the spring.

FEEDING ECOLOGY AND DIET
Atlantic mackerel are opportunistic carnivores that swallow their food whole. Food is captured by active pursuit or by passive filtration with the gill rakers. Juveniles feed on zooplankton. Adults also eat crustaceans but add squids and small fishes to their diet.

REPRODUCTIVE BIOLOGY
In the western North Atlantic, spawning takes place from Chesapeake Bay to Newfoundland, beginning in the south in spring and progressively extending northward into the summer. Most spawning occurs within 10–30 mi (16–48 km) of shore. Mackerel do not begin spawning until the water has warmed to approximately 46.4°F (8°C). The chief production of eggs takes place at temperatures of 48.2–57.2°F (9–14°C). Maturity is attained at 2–3 years of age. Estimates of fecundity range from 285,000 to 1.98 million eggs for females 12–17 in (307–438 mm) fork length. The eggs are 0.04–0.05 in (1.09–1.39 mm) in diameter, have one oil globule, and generally float in the surface water layer above the thermocline.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Mackerel are delicious fish but do not keep as well as fishes that have less oil in their tissues. There are important fisheries in the northwest Atlantic, northeast Atlantic, and Mediterranean and Black seas. FAO catch statistics for 1991–2000 show catches of 6.16–9.42 thousand tons (5.59–8.55 thousand metric tons) per year by 36 countries. Atlantic mackerel are caught mainly with purse seines. Mackerel also are taken by anglers; the all-tackle world record is a 3-lb (1.2-kg) fish taken off Norway. ◆

King mackerel
Scomberomorus cavalla

FAMILY
Scombridae

TAXONOMY
Scomberomorus cavalla (Cuvier, 1829). Based on Marcgrave's guarapucu, Brazil.

OTHER COMMON NAMES
French: Thazard barre; Spanish: Carite lucio.

PHYSICAL CHARACTERISTICS
Maximum size 98 in (250 cm) fork length and 79–99 lb (36–45 kg), commonly to 28 in (70 cm). Body elongate, strongly compressed. Snout much shorter than rest of head. Posterior portion of maxilla exposed, reaching to a vertical with hind margin of eye. Gill rakers on first arch few, 6–11, usually 8–10. Two dorsal fins, scarcely separated, the first with 14–16 spines. Eight or nine dorsal finlets; 9 or 10 anal finlets. Lateral line abruptly curving downward below second dorsal fin. Body completely covered with small scales; no anterior corselet developed. Vertebrae, 41–43. Back iridescent bluish green, sides silvery, adults do not have bars or spots, but juveniles may have spots on sides. Unlike many other species of Spanish mackerels, adults have no black area in the first dorsal fin.

DISTRIBUTION
Confined to the western Atlantic Ocean from Massachusetts to Rio de Janeiro.

HABITAT
Epipelagic and neritic, often found in outer reef areas.

BEHAVIOR
King mackerel are present throughout the year off Louisiana in the Gulf of Mexico, southern Florida, and the state of Ceará in northeastern Brazil. Large schools of king mackerel migrate north along the coast of the United States in spring and return south during the fall.

FEEDING ECOLOGY AND DIET
As for other members of the genus, food consists largely of fishes and small quantities of penaeid shrimps and squids. Various herring-like fishes are particularly important components of the diet.

REPRODUCTIVE BIOLOGY
Spawning takes place from May through September in the western Gulf of Mexico, particularly in September at depths between 115 and 591 ft (35 and 180 m) over the middle and outer continental shelf. In Brazil, fecundity of females 25–48 in (63–123 cm) fork length ranges from 345,000 to 2,280,000 eggs.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
King mackerel is an important species for recreational, commercial, and artisanal fisheries throughout their range. Eight nations reported to FAO catches of 6.0–13.1 thousand tons (5.4–11.9 thousand metric tons) per year from 1991 to 2000, but several other countries combine king mackerel with other species of Spanish mackerel, so the total catch and the number of countries fishing for this species is higher. Commercial fisheries in the southeastern United States use hook-and-line, snapper hooks, gill nets, and trolled lure or small cut bait. In Brazil, gill nets and trolling are major ways of catching king mackerel. In the United States, sport fishing with hook-and-line is practiced in North Carolina, Florida, Mississippi, and Louisiana. The all-tackle world game fish record is a 94-lb (42.18-kg) fish caught off San Juan, Puerto Rico. ◆

Albacore
Thunnus alalunga

FAMILY
Scombridae

TAXONOMY
Thunnus alalunga (Bonnaterre, 1788), Sardinia.

OTHER COMMON NAMES
French: Germon; Spanish: Atún blanco.

PHYSICAL CHARACTERISTICS
Maximum fork length 50 in (127 cm). A large tuna, deepest at a more posterior point than in other tuna species, at or only slightly anterior to second dorsal fin. Two dorsal fins, separated by only a narrow interspace, the first with 11–14 spines, the second with 12–16 rays; anal fin with 11–16 rays; both second dorsal and anal fins followed by seven to nine finlets. Pectoral fins remarkably long, usually 30% of fork length or longer, reaching posteriorly well beyond origin of second dorsal fin. Teeth small and conical, in a single series. Gill rakers, 25–31. Caudal peduncle very slender with a strong lateral keel between two smaller keels. Corselet of large scales anteriorly; rest of body covered with small scales. Swim bladder present. Ventral surface of liver striated. Back metallic dark blue; lower sides and belly silvery white; second dorsal and anal fins yellow; anal finlets dark; white margin on posterior margin of caudal fin.

DISTRIBUTION
Cosmopolitan in tropical and temperate waters of all oceans and Mediterranean Sea, north to 45–50°N, south to 30–40°S. Offshore often extend into cooler waters.

HABITAT
Epipelagic and mesopelagic zones of ocean; abundant in surface waters of 60.1–66.9°F (15.6–19.4°C). Deeper-swimming large albacore are found in waters of 55.9–59.4°F (13.3–15.2°C).

BEHAVIOR
Throughout their range, albacore migrate over great distances and appear to form separate groups at different stages of the life cycle. At least two stocks, northern and southern, are believed to exist in both the Atlantic and Pacific oceans.

FEEDING ECOLOGY AND DIET
Feeds on crustaceans, fishes, and squids.

REPRODUCTIVE BIOLOGY
Albacore tend to spawn in subtropical waters, although they do spawn in tropical waters in some places. Albacore mature at approximately 5 years of age and 35 in (90 cm) fork length in the Atlantic Ocean. Fecundity increases with size generally. A 44-lb (20-kg) female may produce 2–3 million eggs per season released in at least two batches.

CONSERVATION STATUS
Listed as Data Deficient by IUCN.

SIGNIFICANCE TO HUMANS
There are important fisheries for albacore in the Atlantic and Pacific oceans. FAO catch statistics for 1991–2000 show catches of 185–280 thousand tons(168–254 thousand metric tons) per year by 59 countries. The highest landings reported for 2000 were by Japan, 69 thousand tons (62.6 thousand metric tons), and Taiwan, 57.0 thousand tons (51.7 thousand metric tons). With increasing effort in surface fisheries, the world catch has been gradually declining, particularly in the Atlantic Ocean. Albacore are caught by four types of fishing operations: long lining, live-bait fishing, trolling, and purse seining. Albacore is packed as "white-meat" tuna. The all-tackle game fish record is an 88-lb (40.0-kg) fish caught in the Canary Islands. ◆

Atlantic bluefin tuna
Thunnus thynnus

FAMILY
Scombridae

TAXONOMY
Thunnus thynnus (Linnaeus, 1758). Pacific bluefin were considered a subspecies of *T. thynnus* for many years but have recently been raised to species level (Collette et al., 2001) as *T. orientalis* Temminck and Schlegel, 1844.

OTHER COMMON NAMES
English: Northern bluefin tuna; French: Thon rouge; Spanish: Atún.

PHYSICAL CHARACTERISTICS
Maximum fork length more than 118 in (300 cm), commonly to 79 in (200 cm). A very large tuna, deepest near middle of first dorsal fin base. Two dorsal fins, separated by only a narrow interspace, the first with 11–14 spines, the second with 12–16 rays; anal fin with 11–16 rays, both second dorsal and anal fins followed by 7–10 finlets. Pectoral fins very short, less than 80% of head length, never reaching the interspace between the dorsal fins. Teeth small and conical in a single series. Gill rakers, 34–41. Caudal peduncle very slender with a strong lateral keel between two smaller keels. Corselet of large scales anteriorly; rest of body covered with small scales. Swim bladder large. Ventral surface of liver striated. Back metallic dark blue, lower sides and belly silvery white; first dorsal fin yellow or bluish, second dorsal reddish brown, anal fin silvery gray, anal finlets dusky yellow edged with black; no white margin on posterior margin of caudal fin.

DISTRIBUTION
North Atlantic Ocean from Labrador and Newfoundland south into Gulf of Mexico and Caribbean Sea. Replaced by the closely related Pacific bluefin tuna in the north Pacific.

HABITAT
Epipelagic, usually oceanic but seasonally coming very close to shore. Bluefin are found in moderately warm seas but are more tolerant of cold water than are most of their relatives. Offshore in the northwest Atlantic, large bluefin are taken at surface temperatures of 43.5–83.8°F (6.4–28.8°C). Tunas have evolved elaborate rete mirabilia, "wonder nets," of capillaries that act as countercurrent heat exchangers. These heat exchangers form thermal barriers that prevent metabolic heat loss and enable bluefin to maintain a high internal temperature, as high as 83.8°F (28.8°C) for a bluefin taken in 45.1°F (7.3°C) water.

BEHAVIOR
Atlantic bluefin migrate long distances from their spawning grounds off Florida in the western Atlantic and in the Mediterranean Sea in the eastern Atlantic. Tag returns show there is some mixing between eastern and western Atlantic but there is ongoing debate about the proportion of individuals that cross the ocean.

FEEDING ECOLOGY AND DIET
Feed on a variety of fishes, crustaceans, and squids.

REPRODUCTIVE BIOLOGY
Onset of maturity is at approximately 4–5 years. Large adults (10 years and older) spawn in the Gulf of Mexico and in the Mediterranean Sea. Females weighing 592–661 lb (270–300 kg) may produce as many as 10 million eggs per spawning season.

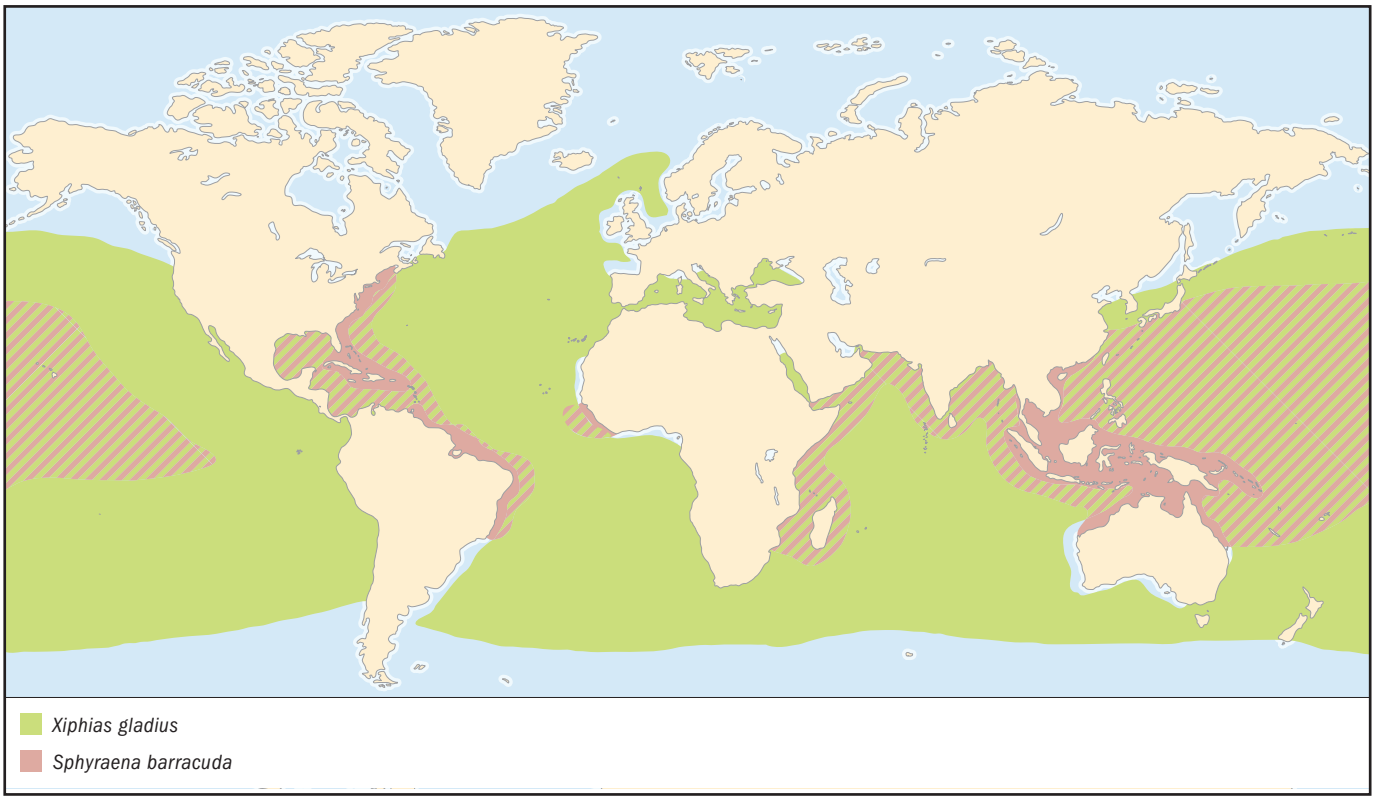
CONSERVATION STATUS
Listed by IUCN as Data Deficient. Western Atlantic bluefin were fished intensively in the 1960s by purse seiners targeting small fish for canneries (Safina, 2001). Obvious depletion led to reduction in the east coast purse seine fleet. Western Atlantic bluefin catches averaged approximately 8,818 tons (8,000 metric tons) during the 1960s and 6,062 tons (5,500 metric tons) during the 1970s. During the 1970s, commercial targeting switched to large fish for export to Japan for sashimi. The offer to buy giant bluefin at $1.45 per pound (0.5 kg) (instead of the previous $0.20 to $0.50 per pound in autumn 1972) greatly increased U.S. fishing pressure on giant bluefin.

SIGNIFICANCE TO HUMANS
Important as both a food fish and a sport fish. FAO catch statistics for 1991–2000 show catches of 29.7–60.2 thousand tons (26.9–54.6 thousand metric tons) per year by 44 countries. The belly meat of bluefin, when containing much fat, reaches astronomical prices in the Japanese market for sashimi. Individual bluefin in prime condition have sold for as much as $68,000, approximately $45 per pound (0.5 kg), but a new record price of $173,600 (¥20 million) was reached for a 444-lb (201-kg) bluefin sold in Tokyo's Tsukiji Central Fish Market in January 2001. The all-tackle game fish record for a "giant" bluefin is a 1,497-lb (679-kg) fish taken off Nova Scotia. ◆

Great barracuda
Sphyraena barracuda

FAMILY
Sphyraenidae

TAXONOMY
Sphyraena barracuda (Walbaum, 1792), West Indies.



OTHER COMMON NAMES
French: Barracuda; Spanish: Picuda barracuda.

PHYSICAL CHARACTERISTICS
Twenty-four vertebrae. Reaches 79 in (200 cm), commonly to 51 (130 cm). Body elongate and slightly compressed. Head large with a long, pointed snout. Mouth large, tip of maxilla reaching to or extending beyond anterior margin of the eye in adults. Lower jaw projecting beyond upper jaw without a fleshy tip. Strong, pointed vertical teeth of unequal sizes in both jaws and in roof of mouth. Two dorsal fins, far apart, the first with five strong spines, its origin slightly behind pelvic fin origin. Tip of adpressed pectoral fin reaching to or extending beyond pelvic fin origin. Gill rakers are absent. Lateral line well developed, straight, with 80–90 scales. Deep green to steel gray above, sides silvery, abruptly becoming white on ventral surface. Adults have several oblique dark bars, usually 18–22, on upper sides and usually have several to many scattered inky blotches on posterior part of lower sides.

DISTRIBUTION
Worldwide in tropical and subtropical waters except eastern Pacific Ocean.

HABITAT
Small individuals are mostly found in shallow waters over sandy and weedy bottoms, often forming schools. Adults usually are solitary dwellers of reef areas and offshore areas.

BEHAVIOR
The fearsome appearance of barracudas combined with voracious feeding behavior and a notable curiosity toward divers has made them one of the most familiar families of marine fishes.

FEEDING ECOLOGY AND DIET
Voracious predators of small fishes, squid, and crustaceans.

REPRODUCTIVE BIOLOGY
Most males mature at two years and all are mature by three years. Some females mature at three years and all are mature at four. The spawning season is from April through October off southern Florida. Females contain 500,000 to 700,000 mature eggs at one time but spawn several times in a season.

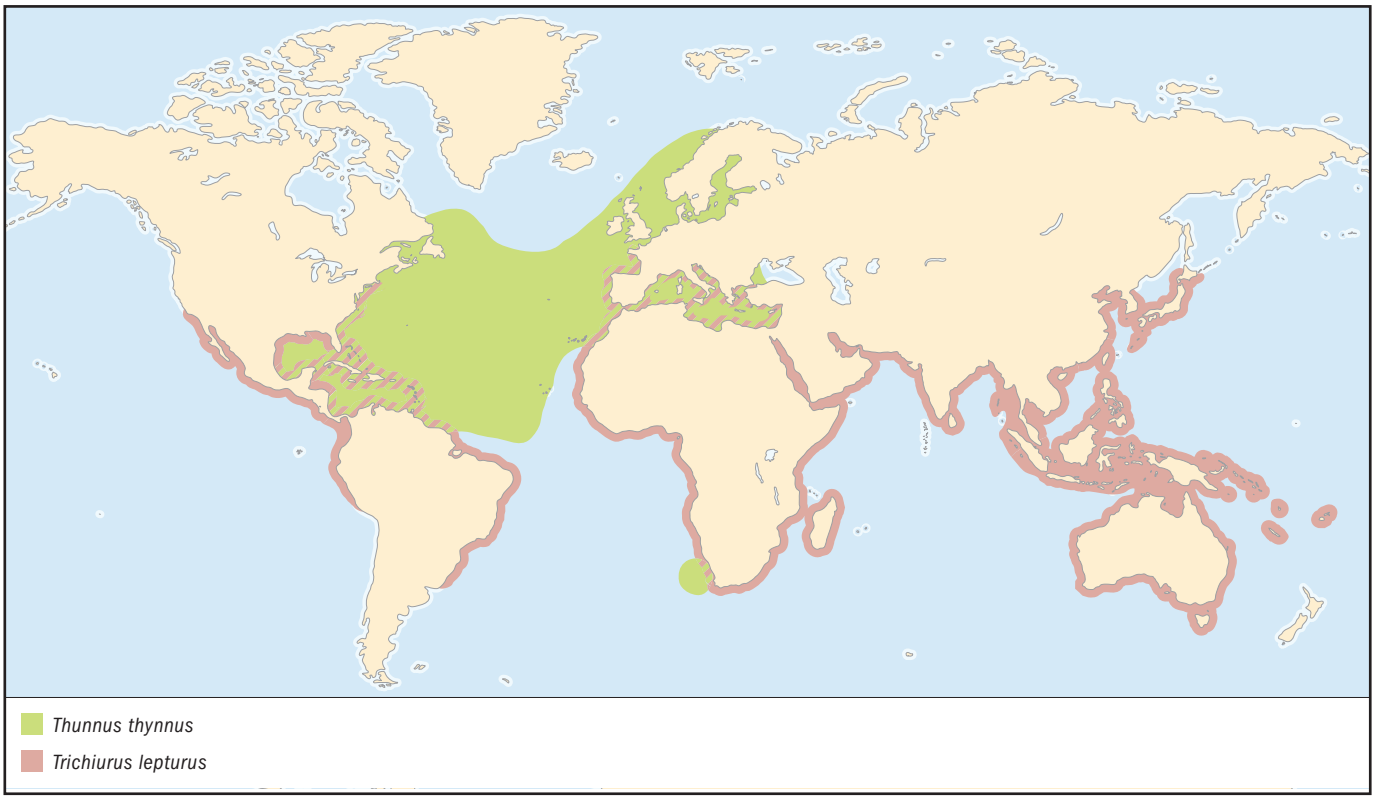
CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Unprovoked attacks on humans have been documented, but they are very rare, and most have occurred because the swimmer was carrying or wearing a silvery, bright object, which a barracuda misidentifies as prey. Human consumption of large individuals may cause ciguatera, a kind of fish poisoning. The toxicity of barracuda flesh is related to the food habits of larger barracuda, which accumulate in their flesh toxin from their prey. There is good evidence that the source of the toxin is a dinoflagellate. Barracuda are not targets of a directed fishery but are caught with hand lines, trolling gear, bottom trawls, gill nets, and trammel nets. Catch data are not reported to the FAO by species; all species of the genus are combined. Marketed fresh and salted. There is a tie for all-tackle game fish record between an 85-lb (38.5-kg) fish from Christmas Island, Kiribati, and one from the Philippines. ◆

Largehead hairtail
Trichiurus lepturus

FAMILY
Trichiuridae

TAXONOMY
Trichiurus lepturus Linnaeus, 1758, South Carolina.



OTHER COMMON NAMES
English: Atlantic cutlassfish; French: Poisson sabre commun; Spanish: Pez sable.

PHYSICAL CHARACTERISTICS
Maximum length 47 in (120 cm) total length, commonly 20–39 in (50–100 cm). Body extremely elongate and strongly compressed, ribbon-like tapering to a point. No caudal fin. Eye large, contained 5–7 times in head length (head length divided by eye diameter equals 5–7). Mouth large with a cartilaginous process at tip of upper and lower jaws. Two or three pairs of enlarged fangs with barbs near tip of upper jaw and another pair near tip of lower jaw. Dorsal fin high and long, no notch between spinous and soft portions, three spines and 130–135 soft rays. Anal fin reduced to 100–105 minute spinules, usually embedded in the skin. Pectoral fins short; pelvic fins absent. Vertebrae numerous, 162–168. Fresh specimens steel blue with silvery reflection, color becoming silvery gray after death.

DISTRIBUTION
Tropical and temperate marine waters of the world if the eastern Pacific *Trichiurus nitens* is regarded as a synonym of *T. lepturus* Nakamura and Parin, 1993.

HABITAT
Benthopelagic, continental shelf to 1,148 ft (350 m), occasionally in shallow waters and at the surface at night.

BEHAVIOR
Juveniles and small adults form schools about 100 m above the bottom during the daytime and form loose feeding aggregations at night-time near the surface. Large adults feed on pelagic prey near the surface during the daytime and migrate to the bottom at night.

FEEDING ECOLOGY AND DIET
Young and immature fish feed mostly on krill, small planktonic crustaceans, and small fishes. Adults become more piscivorous and feed on a wide variety of fishes plus squids and crustaceans.

REPRODUCTIVE BIOLOGY
In the Gulf of Mexico, spawning occurs offshore at depths greater than 151 ft (46 m). The fish mature at 2 years of age and a size of approximately 12 in (30 cm) preanal length for females and 11 in (28 cm) for males. Adult females produce 33,000–85,000 eggs. Eggs are pelagic with a diameter of 0.067–0.074 in (1.7–1.9 mm) and hatch in 3–6 days.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
An important food fish in many parts of the world. FAO catch statistics for 1991–2000 show catches of 867,145–1,631,253 tons (786,661–1,479,848 metric tons) per year by 44 countries in 11 FAO fishing areas. Caught with a variety of nets. Also taken by anglers; the all-tackle world record is an 8-lb (3.7-kg) fish taken off Rio de Janeiro. ◆

Swordfish
Xiphias gladius

FAMILY
Xiphiidae

TAXONOMY
Xiphias gladius Linnaeus, 1758, European seas.

OTHER COMMON NAMES
French: Espadon; Spanish: Pez espada.

PHYSICAL CHARACTERISTICS
Reaches a maximum size of 175 in (445 cm) total length and approximately 1,190 lb (540 kg). The body is elongate and cylindrical. Two widely separated dorsal fins in adults, the first much larger than the second, the first with 34–49 rays, the second with four to six rays. Two separate anal fins in adults, the first with 12–16 rays, the second with three or four rays. Pectoral fins falcate, located low on body sides, with 17–19 rays. Caudal fin large and lunate, with a deep notch on upper and lower profiles of caudal peduncle. Fine file-like teeth and scales with small spines are present in juveniles but become embedded in the skin with growth at approximately 3 ft (1 m) in length. Left and right branchiostegal membranes separated distally. Vertebrae, 26. Back and sides of body blackish brown, gradually fading to light brown on ventral side.

DISTRIBUTION
Cosmopolitan in tropical, temperate, and sometimes cold waters of all oceans, including the Mediterranean, Black, and Caribbean seas.

HABITAT
This is an epipelagic and mesopelagic, oceanic species, usually found in surface waters warmer than 55.4°F (13°C), the optimum temperature range being 64.4–71.6°F (18–22°C). Swordfishes have been acoustically tracked and directly observed from submersibles in the western Atlantic and eastern Pacific to depths of 2,024 ft (617 m).

BEHAVIOR
It is likely that swordfishes use the sword to stun or kill some prey, as shown by slashes on the bodies of squid and fishes found in swordfish stomachs. The brain and eyes of swordfish are warmer than the water in which they live. The tissue that heats the brain is developed from the superior rectus muscle of the eye. The brain heater protects the central nervous system from rapid cooling during vertical excursions of as much as 984 ft (300 m) that these fish may make through a temperature range as great as 34.2°F (19°C) in 2 hours.

FEEDING ECOLOGY AND DIET
Adult swordfishes are opportunistic feeders, known to forage for their food from the surface to the bottom over a wide depth range. Over deep water, they feed primarily on pelagic fishes including tuna, dolphinfishes, lancetfishes, flyingfishes, and pelagic squids. In shallow waters swordfishes often take neritic pelagic fishes such as mackerel, herring, anchovies, sardines, and sauries. Large adults may make feeding trips to the bottom for demersal fishes.

REPRODUCTIVE BIOLOGY
In the western Atlantic, spawning apparently occurs throughout the year in the Caribbean, the Gulf of Mexico, and waters off Florida. Swordfishes spawn in the upper water layers at depths of 0–246 ft (0–75 m) and temperatures of approximately 73.4°F (23°C). Swordfishes first spawn at 5 or 6 years of age and 59–67 in (150–170 cm) eye-fork length and lay 2–5 million eggs.

CONSERVATION STATUS
Listed by IUCN as Data Deficient. Populations of swordfish have been greatly reduced by fishing, particularly in the Atlantic Ocean. A consumer boycott of Atlantic swordfish organized by the United States–based Natural Resources Defense Council and Sea Web affected prices enough to gather crucial momentum toward a recovery plan for depleted swordfish in the Atlantic (Safina, 2001).

SIGNIFICANCE TO HUMANS
Appreciation of swordfish as a food fish is recent. Swordfishes brought only approximately $0.24 per pound (0.5 kg) in 1919 and $0.60 in 1946. There are important fisheries for swordfish in all three major oceans. Swordfishes are caught by long line, harpoon, drift gill net, set nets, and other fishing gear. FAO catch statistics for 1991–2000 show catches of 76–116 thousand tons (69–105 thousand metric tons) per year by 77 countries. Restrictions on the sale of swordfish containing levels of mercury greater than 0.5 ppm in Canada and the United States in the early 1970s caused collapse of the Canadian fishery and severely restricted landings in the United States. The mercury guidelines were raised to 1.0 ppm in 1979, and by 1980 catch and effort had reached a new high in the northwest Atlantic. Swordfishes are important sport fishes. The all-tackle game fish record is a 1,182-lb (536.2-kg) fish taken off Chile. ◆

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Organizations

Inter-American Tropical Tuna Commisssion. 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508 USA. Phone: (858) 546-7100. Fax: (858) 546-7133. Web site: <http://www.iattc.org>

International Commission for the Conservation of Atlantic Tunas. Calle Corazón de Maria, 8, 6th floor, Madrid, E-28002 Spain.

Bruce B. Collette, PhD

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Stromateoidei
(Butterfishes and relatives)

Class Actinopterygii
Order Perciformes
Suborder Stromateoidei
Number of families 6

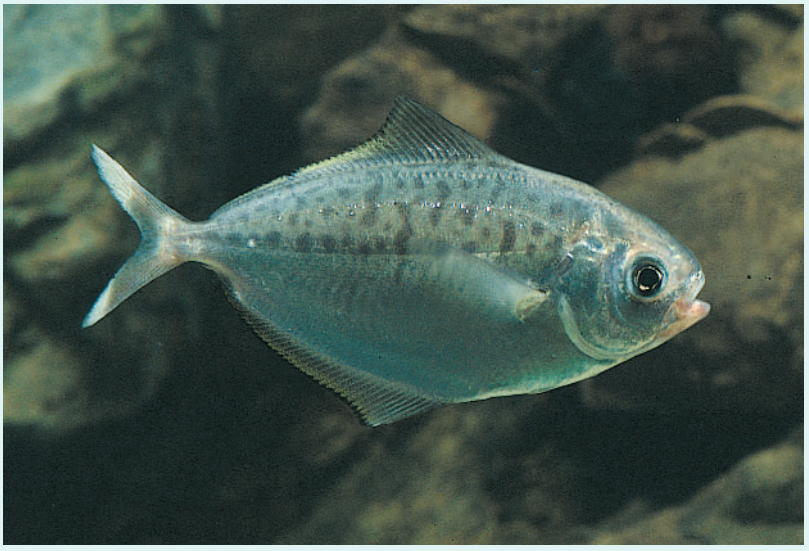


Photo: The butterfish (*Peprilus triacanthus*) is a small schooling fish that is found off the East Coast of the United States. They are named for their flavor, not their appearance. (Photo by Animals Animals ©Zig Leszczynski. Reproduced by permission.)

Evolution and systematics

The fossil record of the Stromateoidei is not very extensive, consisting mostly of isolated otoliths, the paired earstones present in the membranous labyrinth of the inner ear of many fishes that can aid in detecting motion. Otoliths are difficult to identify because they usually lack the diagnostic features of families of fishes. Irrespective of this, the earliest otoliths attributed to a stromateoid date from the early Tertiary period (about 50 million years ago), of France, Belgium, and England. Fossils known from more than otoliths, such as skeletons, are rare, and these are also fragmentary, such as *Psenicubiceps alatus* from Russia, currently assigned to the stromateoid family Nomeidae. The earliest stromateoid fossils are believed to be from Denmark, from deposits as old as 60 million years, but these cannot presently be assigned with confidence to the Stromateoidei.

The Stromateoidei is a suborder of the large bony fish order Perciformes. The composition of this suborder has changed only slightly in the past 35 years; it was mostly assembled in a landmark study in 1966 by Humphry Greenwood, Donn E. Rosen, Stanley H. Weitzman, and George S. Myers, in which all families were grouped together except the Amarsipidae, which was added in 1969. The Stromateoidei currently includes 6 families, 15 genera, and some 65 species. The families are: Amarsipidae (with a single genus and species, *Amarsipus carlsbergi*), Nomeidae (driftfishes; 3 genera and 15 species), Centrolophidae (medusafishes; 7 genera and 27 species), Tetragonuridae (squaretails; 1 genus, *Tetragonurus*, and 3 species), Stromateidae (butterfishes; 3 genera and 13 species), and Ariommatidae (1 genus, *Ariomma*, and 6 species).

Within the Perciformes, stromateoids are more closely related to certain generalized families that share a specific arrangement of the ramus lateralis accessorius (a facial nerve complex), including the Kyphosidae, Girellidae, Scorpididae, Arripididae, Kuhliidae, Microcanthidae, Oplegnathidae, and Terapontidae. Of these families, the stromateoids are more closely related to the Kyphosidae (chubs), sharing with them details of their tooth pattern and larval pigmentation. Evolutionary relationships within the Stromateoidei indicate that the Amarsipidae are the most basal group, that the Centrolophidae may not have unique features, and that the butterfishes (Stromateidae) are the most derived stromateoids.

Physical characteristics

Stromateoids are moderate-sized fishes up to 47.2 in (1.2 m) in length, generally with round and somewhat large eyes (with associated adipose tissue in ariommas), small mouths, forked caudal fins (with 15 branched rays), and elongated dorsal fins that may be continuous or subdivided. The body is slender to deep, and is either compressed laterally or rounded in cross-section. The dorsal fins have spines (weak in some species); an anal fin with one to three spines; the dorsal and anal fins generally terminate at the same level; pelvic fins are absent in adults of some species (e.g., butterfishes, although the pelvic bones are present); pelvic fins are small in others, and very large in the man-of-war fish (*Nomeus gronovii*). The jaw teeth are small, usually arranged in a single series; the nostrils are double; a lateral line is present. The gill rakers range from 10–20 on the first gill arch. Scales are usually cycloid. Coloration may vary from silvery to dark brown in adults, but is usually mottled in juveniles. Some species have more elaborate color patterns, with blotches and bands.

Stromateoids, with the exception of the Amarsipidae, are unique in having a specialized pharyngeal organ (the pharyngeal sac) just anterior to the esophagus and following the last

gill arch, which is specialized for further breaking down food items. The pharyngeal sacs are coated internally by small projections (papillae) that contain minute "teeth"; the structure and arrangement of the papillae vary significantly among species. All stromateoids share a specific configuration of the internal caudal fin skeleton.

Distribution

Stromateoids are found in all major oceans (except the Arctic, Baltic, Okhotsk, and Black Seas, and the Antarctic Ocean) from the high seas well offshore, to the continental shelf regions, and in large bays. They are more common in temperate and tropical waters, but a few species also occur in colder areas. Many offshore pelagic species are very widely distributed.

Habitat

All stromateoid species are marine. Some eight genera are oceanic, six genera are mostly coastal, and two are both coastal and oceanic. As a general rule, young individuals are usually epipelagic, sometimes living in association with jellyfishes, but adults occur mostly in deeper waters, either demersally (inshore or offshore down to about 1,640 ft/500 m); more in some species, but usually in shallower waters) or mesopelagically.

Behavior

The behavior of individual stromateoids, other than in relation to their association with jellyfishes, is virtually unknown. Many species form schools of moderate size, as individuals are frequently captured together. The association between stromateoids (usually juvenile) and jellyfishes requires further study, but it appears to form very early in the fish's development. Stromateoids are more resistant to jellyfish toxins than other fishes. They may also associate with salps (semitransparent barrel-shaped marine invertebrate animals), where juveniles of squaretails may seek refuge. They usually hover underneath the bell of the jellyfish, but may swim in and out of its tentacles to snatch prey items (mostly zooplankton and other invertebrates). They may also feed occasionally on the tentacles and gonads of the jellyfish, and are also subjected to predation by them. Juveniles in association with jellyfishes are usually more colorful or display more complex color patterns than adults of the same species, which are usually demersal or pelagic. Individuals of some species (e.g., the barrelfish, *Hyperoglyphe perciformis*) may congregate under floating wreckage, oceanic flotsam, planks, buoys, or other sheltered mobile habitats. Others may gather around vessels.

Feeding ecology and diet

Food items consist mostly of invertebrates (numerous crustaceans, such as barnacles, crabs, shrimps, and euphausiids (small shrimp-like crustaceans), in addition to squids, various other mollusks, and zooplankton), but many species have a predilection for jellyfishes. Small fishes may be taken occasionally, as well as urochordates. Stromateoids are preyed upon by larger fishes, including sharks, and also by their jellyfish hosts.

Reproductive biology

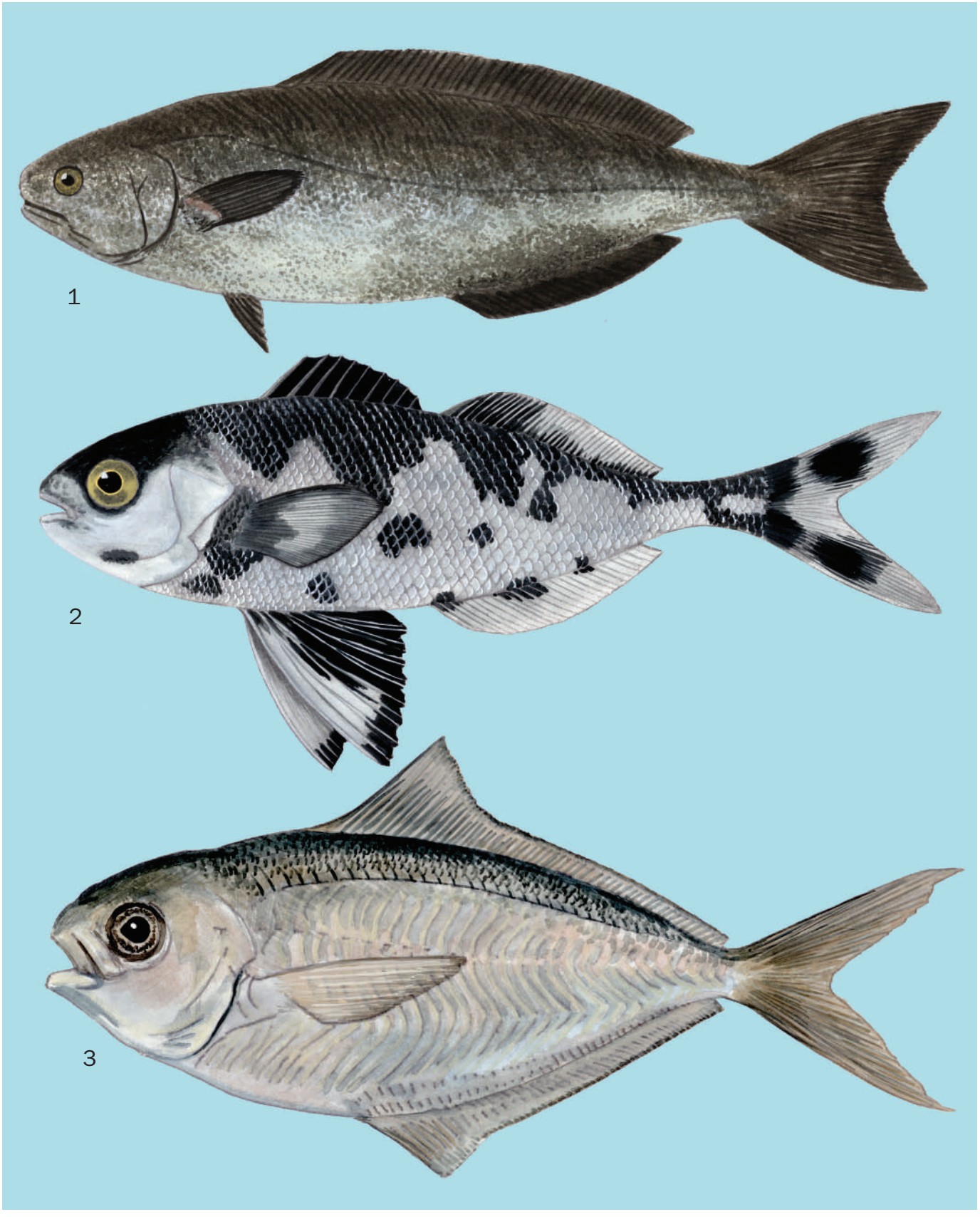
As with many pelagic fishes, stromateoids are broadcast spawners, releasing large quantities of eggs into the pelagic realm upon spawning. Spawning may occur on a yearly basis during the summer months in some species, but spawning periods are unrecorded for many stromateoids. The eggs are small, ranging from 0.03–0.07 in (about 0.07–0.18 cm) in diameter, when known; they are spherical, separate, and pelagic; and usually contain a single oil droplet. Hatching usually occurs under 0.2 in (0.5 cm) in length, and flexion takes place shortly thereafter. Depending on the species, juveniles begin to resemble adults at about twice their flexion length. The eggs and larvae of about one-half of all stromateoid species have yet to be described.

Conservation status

No species are listed by the IUCN.

Significance to humans

Some stromateoid species are of commercial importance locally, especially in Japan and Southeast Asia. Among the most important species are the silver pomfret (*Pampus argenteus*), with a yearly catch ranging from 11,000 to 18,000 tons (11,177–18,289 t) between 1990 and 1995; the Indian ariomma (*Ariomma indicum*), with a yearly catch reported at 9,000 tons/9,144 t off Africa; and the American butterfish (*Peprilus triacanthus*). Most other species are of little or no importance commercially. All species are harmless.



1. Black ruff (*Centrolophus niger*); 2. Man-of-war fish (*Nomeus gronovii*); 3. Butterfish (*Peprilus triacanthus*). (Illustration by Dan Erickson)

Species accounts

Black ruff
Centrolophus niger

FAMILY
Centrolophidae

TAXONOMY
Perca nigra Gmelin, 1788, eastern Atlantic.

OTHER COMMON NAMES
English: Blackfish; French: Centrolophe noir; German: Schwarzfisch; Spanish: Romerillo.

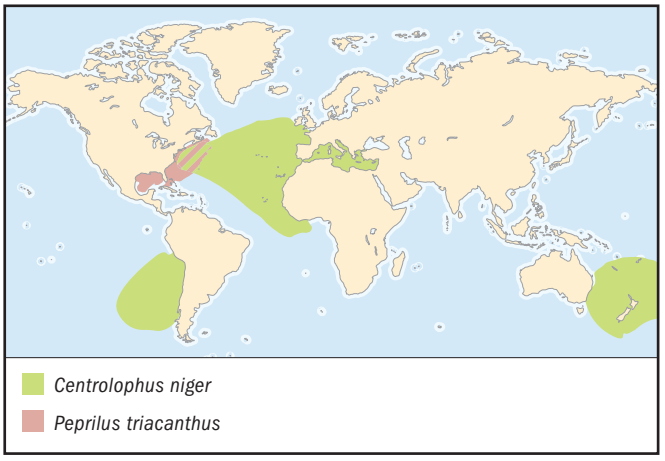
PHYSICAL CHARACTERISTICS
Length 43.3 in (110 cm). Elongate, with a rather small head and large eyes; continuous dorsal fin extends most of the length of the body (with 4–5 weak spines and 32–38 rays); anal fin with 3 spines and 20–27 rays; pelvic fins small, under pectorals; pectorals with 19–23 rays; caudal fin weakly forked; mouth rather wide, extending posteriorly beneath eyes; coloration dark bluish gray, but sometimes darker.

DISTRIBUTION
Western (from Nova Scotia to New Jersey) and eastern North Atlantic, Mediterranean Sea, and also the Pacific Ocean off Australia, New Zealand, and South America.

HABITAT
Temperate oceanic waters. Young specimens occur near surface; larger individuals are mesopelagic. Specimens have been captured as deep as 1,968 ft (600 m) off Australia and New Zealand.

BEHAVIOR
Little is known concerning its behavior. Small specimens have been found in association with jellyfishes, but adults may form schools.

FEEDING ECOLOGY AND DIET
Feeds on jellyfishes, squids, and different kinds of crustaceans. Preyed on by hake and possibly other larger fishes.



REPRODUCTIVE BIOLOGY
Eggs and larvae are pelagic; eggs are spherical, small (0.05 in/0.12 cm in diameter) and contain a single oil globule. Hatching occurs at about 0.16 in (0.4 cm) standard length, flexion at 0.2 in (0.6 cm), adult body form attained at 0.7 in (1.7 cm). Growth reported to be relatively fast. Probably a broadcast spawner.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Not significantly consumed and therefore of minor importance. ◆

Man-of-war fish
Nomeus gronovii

FAMILY
Nomeidae

TAXONOMY
Gobius gronovii Gmelin, 1788, eastern Atlantic.

OTHER COMMON NAMES
English: Bluebottle fish, shepherd fish; Spanish: Pastorcillo, Pez azul.

PHYSICAL CHARACTERISTICS
Standard length 13.7 in (35 cm). Head somewhat tall, body tallest at level of pelvic fins, tapering posteriorly; dorsal fin continuous, originating at midbody length, with 9–12 spines and 25–27 rays (IX–XII, 24–28); pectoral fins elongate, with 21–23 rays; caudal fin forked, with some 15 rays; anal fin with two spines and 24–29 rays (I–II, 24–26); pelvic fins very long and prominent, reaching posteriorly to level of pectoral fin extremities, with one spine and five rays (I, 5); eyes large; no teeth on tongue. Juveniles have vertical, dark blue and broad bands, with blue blotches on head and fins; adults have irregular blue blotches on body, head, and fins; background color silvery, pelvic and dorsal fins black. Larger adults more uniformly dark in color.

DISTRIBUTION
Tropical and warm temperate waters of Atlantic, Pacific, and Indian Oceans.

HABITAT
Pelagic offshore, usually warm waters, commonly found in association with the siphonophore Portuguese man-of-war (*Physalia*), but larger adults may live independently in deeper waters. Juveniles may be found pelagically in waters 98 ft (30 m) deep.

BEHAVIOR
Usually found in large numbers living underneath the bell of the Portuguese man-of-war, swimming in and out among its tentacles. The mottled color pattern mimics the tentacles of *Physalia*. It lives commensally by being resistant to the venom of the siphonophore.

FEEDING ECOLOGY AND DIET
Feeds on the tentacles and gonads of the Portuguese man-of-war, zooplankton, and other soft-bodied jellyfishes. Sometimes eaten by its host.

REPRODUCTIVE BIOLOGY
Eggs and preflexion larvae are unknown; postflexion larvae as small as 0.27 in (0.7 cm) have been recorded, and adult form is mostly attained by 0.9 in (2.5 cm). Other aspects of its reproduction are unknown, but as with other stromateoids, eggs and larvae are pelagic and they are probably broadcast spawners. Small individuals of 0.39 in (1 cm) have been found in association with the Portuguese man-of-war, indicating that this association forms early in life.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Of minor commercial importance, due to infrequent fishing. ◆

Butterfish
Peprilus triacanthus

FAMILY
Stromateidae

TAXONOMY
Stromateus triacanthus Peck, 1804, New Hampshire, United States.

OTHER COMMON NAMES
English: American butterfish; French: Stromaté fossette; Spanish: Palometa pintada.

PHYSICAL CHARACTERISTICS
Length about 11.8 in (30 cm). Body thin and deep, with short head and blunt snout. Single dorsal fin is taller shortly posterior to its origin, with 2–4 spines and 40–48 soft rays (II–IV, 40–48); pectoral fins moderately elongate with 1–22 fin rays; 22–25 gill rakers; lateral-line scales 96–105; anal fin almost as long as dorsal fin, with 3 spines and 37–44 rays; caudal fin deeply forked with slightly greater lower lobe. Pelvic fins absent. Color grayish blue above and silvery on sides, with many irregular dark spots laterally.

DISTRIBUTION
Western Atlantic Ocean, from off South Carolina, United States, to Nova Scotia (sometimes as a stray off the coast of Newfoundland); also further south to the coast of Florida, United States, in deeper water, as well as in the Gulf of Mexico.

HABITAT
Continental shelf; found pelagically or demersally in waters as deep as 600 ft (183 m), usually over sandy bottoms. May venture into shallow bays and estuaries.

BEHAVIOR
Little is known concerning behavior other than reproduction. During the first year may live in association with jellyfishes or freely, but forms schools as adults. Migratory patterns are common in consequence of water temperature. Appear seasonally off northeastern coast of the United States, but are generally unpredictable as to when.

FEEDING ECOLOGY AND DIET
Feeds abundantly on soft-bodied invertebrates, preferring urochordates and mollusks. Also feeds on cnidarians, ctenophores,

chaetognaths, polychaetes, and crustaceans (including amphipods, copepods, mysids, and euphausiids). Juveniles in Narragansett Bay, Rhode Island, United States, feed heavily on ctenophore *Mnemiopsis leidyi*, not by ingesting it whole but by taking small bites. Feeding occurs both day and night. Preyed on by some 30 species of fishes and squids, and are part of the diet of many commercially important fishes, such as haddocks, bluefishes, swordfishes, summer flounders, and hammerhead sharks.

REPRODUCTIVE BIOLOGY

Sexually mature between first and second years, starting about 7.1 in (18 cm) standard length (i.e., exclusive of the caudal fin). Broadcast spawners, lack specialized courtship behavior. Spawning takes place once a year during summer months. Eggs are buoyant, spherical, and transparent, measure some 0.03 in (0.08 cm) in diameter; include a single oil droplet. Larvae begin to resemble adults about 0.6 in (1.5 cm), when fin rays of dorsal, anal, and caudal fins are fully formed.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Important commercial fishes, heavily consumed since the 1800s, and commonly caught by otter trawls, gill nets, and other means. In the early 2000s, yearly catches averaged under 4,921 tons (5,000 t), but in 1973 close to 19,684 tons (20,000 t) were landed. The flesh is considered to be very delicious and "melt-in-your-mouth," which is reflected in the common name. ◆

Resources

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Marcelo Carvalho, PhD

Anabantoidei
(Labyrinth fishes)

Class Actinopterygii
Order Perciformes
Suborder Anabantoidei
Number of families 3

Photo: This thick-lipped gourami (*Colisa labiosa*) variety is bred for the aquarium trade. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The labyrinth fishes were first recognized as a natural assemblage by Cuvier and Valenciennes in 1831, but included the Channidae (snakeheads), in addition to the current family Anabantoidei. Bleeker (1859, 1879) added the luciocephalids (pikeheads) to this group. Jordan (1923) recognized six families, including *Luciocephalus* and Channidae. In 1963, Liem restricted the anabantoids to the families Anabantidae, Helostomatidae, Osphronemidae, and Belontiidae, thus removing *Luciocephalus* and the channids. In 1983 Lauder and Liem included *Luciocephalus*, in its own family Luciocephalidae, again in the anabantoids as the sister group to all remaining labyrinth fishes. Britz (1994, 1995), and Britz et al. (1995) demonstrated that there are no differences between Liem's families Belontiidae and Osphronemidae and that *Luciocephalus* is deeply nested within Liem's belontiids. The family name Osphronemidae applies for this monophyletic assemblage. The suborder Anabantoidei is thus divided into three families, Anabantidae, Helostomatidae, and Osphronemidae. The latter family is the sister group of the former two, and it is further subdivided into the subfamilies Belontiinae (only *Belontia*, two spp.); Osphroneminae (only *Osphronemus*, four spp.); Luciocephalinae (*Trichogaster*, four spp.; *Colisa*, four spp.; *Parasphaerichthys*, two spp.; *Ctenops*, one sp.; *Sphaerichthys*, four spp.; *Luciocephalus*, one sp., one undescribed sp.); and Macropodinae (*Macropodus*, five spp.; *Pseudosphromenus*, two spp.; *Malpulutta*, one sp.; *Parosphromenus*, 10 spp., some undescribed; *Trichopsis*, three spp.; *Betta*, 43 spp., some undescribed).

The closest relatives of anabantoids appear to be the Channidae. Based on the shared presence of parasphenoid teeth, both seem to form a larger monophyletic group with the badids and the genera *Nandus* and *Pristolepis*. The only unambiguous fossil anabantoid is a complete articulated skeleton from the Miocene epoch of Sumatra, assigned to *Osphronemus goramy*.

Physical characteristics

Anabantoids are minute (0.78 in; 20 mm) to large (23.6 in; 60 cm) percomorph fishes with a suprabranchial organ as accessory air-breathing organ. This organ consists of the suprabranchial chamber above the gill arches that houses the modified first epibranchial, termed the labyrinth. The labyrinth may have a highly complex three-dimensional shape in some species (*Anabas* and *Osphronemus*). Both the labyrinth and the wall of the suprabranchial chamber are lined with respiratory epithelium. The suprabranchial organ obtains blood from the first two afferent branchial arteries. Blood from the organ is collected in the two anterior efferent arteries that drain into the anterior cardinal vein, not into the dorsal aorta as in other teleosts. Basioccipital with paired articular processes that permit free movement with upper pharyngeal jaws. The last two characters are shared with the channids. In most anabantoids, the lacrimal and preopercular bones bear strong serrations; in anabantids, serrations occur in the subopercle, opercle bones, and sometimes the interopercle. (The name *anabantids* is vernacular for the family Anabantidae; *anabantoids* is the vernacular name for the suborder Anabantoidei.) All species except African anabantids and *Helostoma* have a exoccipital foramen medial to suprabranchial chamber, greatly enhancing hearing abilities. Most species are parasphenoid toothed, a unique derived character shared with channids, badids, *Nandus*, and *Pristolepis*. The swim bladder branches off posteriorly into two elongate diverticula that reach on either side of the hemal spines to the level of the parhypural. Many species are beautifully colored, with striking sexual dimorphism and dichromatism.

Distribution

Anabantoids occur in fresh waters of sub-Saharan Africa, and south and Southeast Asia. The genera *Ctenopoma*, *Microctenopoma*, and *Sandelia* occur only in Africa. The latter genus is confined to the Cape region and separated by a distributional gap from the other African anabantids. Most Asian species are widely distributed, but some have a greatly restricted distribution, such as *Belontia signata* and *Malpulutta kretseri*, known only from Ceylon, or *Parosphromenus deissneri*, *Betta miniopinna*, *B. schalleri*, *B. burdigala*, and *B. chloropharynx*, restricted to Banka Island in Indonesia. The

The dwarf gourami (*Colisa lalia*) is found in waters from northeastern India to Bangladesh. (Photo by Mark Smith/Photo Researchers, Inc. Reproduced be permission.)

northernmost distributed species is *Macropodus ocellatus*, from China and Korea.

Several species have been exported as food fishes or have been released accidentally from aquarium stocks to areas outside their natural ranges.

Habitat

Numerous species of anabantoids prefer still bodies of water with abundant aquatic vegetation that are exposed to the sun, but others also live in cooler, faster, mountain streams. Most anabantoids survive in oxygen-depleted waters because of their suprabranchial organ and therefore have an advantage over most other teleosts.

Behavior

In general, anabantoids differ from most other teleosts in that they rise to the water surface at intervals to exchange the air in their suprabranchial organ. This exchange is mostly achieved by flooding the suprabranchial chamber with water that enters through the gill opening. The water pushes the air out of the chamber and the mouth, either before or upon reaching the water surface. The chamber refills with air breathed in at the surface. In a second mode, air is gulped from the surface without the prior release of air from the chamber. Engulfed air is then pressed into the chamber by swallowing movements and forces some air out of the chamber, which is released from the gill opening. The latter mode is used by adult *Anabas testudineus* in the water and during the overland excursions that gave the species its vernacular name, the climbing perch. In addition to the climbing perch, at least one other anabantid species, the African *Ctenopoma multispinis* actively leaves the water and travels over land to nearby bodies of water.

Species of the genus *Colisa* show a behavior reminiscent of the spitting of the archerfishes (*Toxotes jaculatrix*). At least in captivity, representatives of *Colisa* spit a series of small droplets of water toward prey items, such as small invertebrates, above the water level to wash them down to the surface where they are taken by the fish.

Species of the genus *Trichopsis* are known for their ability to produce croaking sounds, hence their name, croaking gourami. These sounds are produced with their pectoral fins. To create the sounds, enlarged areas of tendons from the pectoral fin musculature are moved across bony knobs on some of the pectoral fin rays. The sound is enhanced by the suprabranchial chambers, which act as resonators.

All anabantoid species, except *Sandelia capensis*, show a typical, and for teleosts unusual, spawning clasp in which the male wraps around the female's body. The female is then either turned to the side or upside down when eggs are released. A similar clasp is also found in channids, badids, and *Nandus*, but not other nandids. A reduced clasp without turning of the female is shown by some mouth-brooding anabantoids.

Feeding ecology and diet

Anabantoids are diverse in regard to their feeding ecology and diet. There are extreme filter feeders, such as *Helostoma*, which feeds on small pelagic invertebrates and algae that are either filtered from the water or scraped off the substrate. Other species are omnivorous (*Anabas*, *Osphronemus*, *Trichogaster*, and *Colisa*), or have a diet with an emphasis on small invertebrates (*Microctenopoma*, *Macropodus*, *Betta*, and *Trichopsis*), but others prey on larger invertebrates and small fishes (*Ctenopoma* and *Sandelia*). *Luciocephalus* is a highly specialized predator of small fishes. *Osphronemus exodon* is an exclusively herbivorous species with external jaw teeth, which feeds on leaves of terrestrial plants, grasses, fruits, and flowers.

Reproductive biology

Although anabantoids are a fairly small percomorph group, their members exhibit a great variety of reproductive modes. The primitive mode, which occurs in *Anabas*, *Ctenopoma*, and *Helostoma*, is the absence of parental care with the release of several thousand small (ca. 0.04 in/1 mm), buoyant eggs that float due to a single large oil globule in the egg. After hatching, larvae retain the oil globule, which during development divides into two oil vesicles to the left and right of the chorda and is used as a floating organ. All species of the genus *Microctenopoma* and most osphronemids build bubble nests and guard primitively buoyant eggs and larvae. Bubble nests can consist of only a few bubbles, as in the tiny cave-brooding species of *Parosphromenus*, or be large. Mouth brooding has evolved at least twice among anabantoids, once in the lineage *Ctenops*, *Sphaerichthys*, and *Luciocephalus*, and again within the genus *Betta*.

Unusually for anabantoids, the two species of the purely South African genus *Sandelia* spawn on a substratum and have adhesive eggs. In groups with parental care, the number of eggs is usually smaller than in those without care, although several thousand eggs may be spawned in some species of *Microctenopoma* and *Trichogaster*. The number of eggs may range from 40 to several hundreds in most bubble nest builders, and

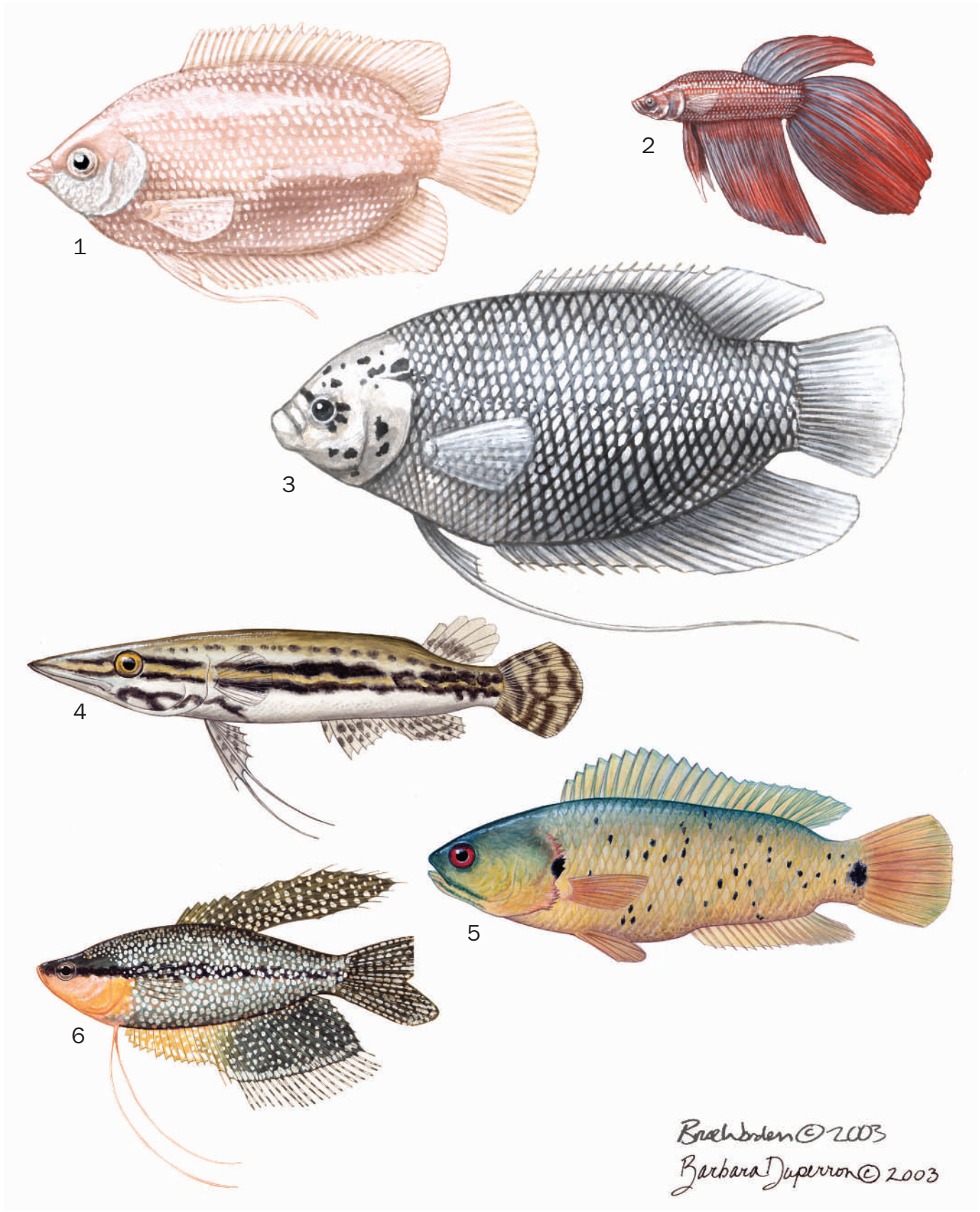
from 20 to 200 in the mouth brooders. Egg size ranges from 0.03 in (0.7 mm) in *Microctenopoma* to 0.19 in (3 mm) in *Luciocephalus*.

Conservation status

Three anabantoid species are categorized as Critically Endangered by the IUCN, *Betta miniopinna*, *Betta persephone*, and *Betta spilotogena*. *Sandelia bainsii*, *Parosphromenus harveyi*, and *Betta livida* are categorized as Endangered. Another seven *Betta* species are categorized as Vulnerable, and the two Sri Lankan species *Belontia signata* and *Malpulutta kretseri* are categorized as Lower Risk.

Significance to humans

The larger species of anabantoid fishes are important as food fishes and feature in aquaculture in various parts of Asia. Many of the smaller, colorful anabantoids are very popular hardy ornamental fishes; up to several hundred U.S. dollars have been paid for a breeding pair of the conspicuously colored fighting fish *Betta macrostoma*, known as the Brunei beauty.



1. Kissing gourami (*Helostoma temminckii*); 2. Siamese fighting-fish (*Betta splendens*); 3. Giant gourami (*Osphronemus goramy*); 4. Pikehead (*Luciocephalus pulcher*); 5. Climbing perch (*Anabas testudineus*); 6. Pearl gourami (*Trichogaster leeri*). (Illustration by Barbara Duperron and Bruce Worden)

Species accounts

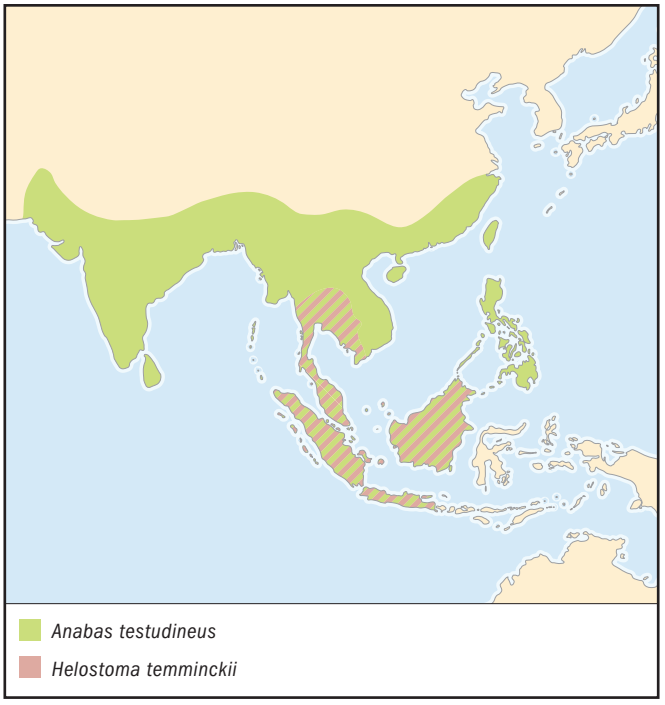
Climbing perch
Anabas testudineus

FAMILY
Anabantidae

TAXONOMY
Anthias testudineus Bloch, 1785, Japan. The diverse distribution and morphology of *A. testudineus* indicate that it may comprise more than one species.

OTHER COMMON NAMES
French: Perche grimpeuse; German: Kletterfisch; Spanish: Perca trepadora.

PHYSICAL CHARACTERISTICS
Length 9.8 in (25 cm). Robust body with wide, large head. Body shape ranges from oval and compressed to elongate and subcylindrical. Posterior edges of opercular bones, especially opercle, and subopercle, with strong spination. Without teeth on the palatine in contrast to most anabantids. Dorsal fin has 16–19 strong spines and 7–11 soft rays. Anal fin has 9–11 spines and 8–12 soft rays. Pelvic girdle without connection to pectoral girdle. Scales on the head rigidly attached to the skull bones. Scales strongly ctenoid. Lateral line interrupted at level of posterior part of spinous dorsal fin and continued two scale rows lower down to caudal peduncle. Suprabranchial organ exceptionally large and complexly folded. Coloration light beige with darker spots. A conspicuous black spot at the posterior edge of the gill cover between two prominent areas of projecting strong opercular spines and a large black ocellus on the caudal peduncle. No sexual dimorphism or dichromatism.



DISTRIBUTION
Widely distributed in Asia: Sri Lanka, India, Burma, Indochina, Taiwan, Sundaland (the western part of Indonesia, namely the islands of Java, Sumatra, and Kalimantan), but also introduced east of Huxley's Line (a zoogeographic distributional divide between the fauna of peninsular Southeast Asia and the Sunda islands [Sumatra, Java, and Borneo], and the fauna located on islands further to the east such as Australia, Papua New Guinea, Sulawesi, and the Philippines). This wide distributional range and the diverse physical morphology encountered indicates that more than one species is most certainly involved, but this species has not been thoroughly studied. The climbing perch has also been accidentally released in the United States.

HABITAT
Found in all types of fresh water, also survives in brackish water and tolerates water conditions unsuitable for most other fishes.

BEHAVIOR
Well known for its behavior to travel overland, first reported more than 200 years ago; uses its spiny opercular bones and a side-to-side wriggling of the body to move itself forward on land. Obligatory air breather that drowns if kept from rising to the surface to gulp air. Can survive longer periods of drought buried in the mud of the drying water bodies.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on macrophytic vegetation, different invertebrates, and small fish.

REPRODUCTIVE BIOLOGY
No parental care. Typical spawning clasp lasts only a few seconds. Several thousand, buoyant, small (0.04 in; 1 mm) spherical eggs are spawned during one spawning phase. Eggs contain a single large oil globule. Hatching occurs after 24 hours at 82.4°F (28°C).

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A common and popular food fish in Southeast Asia. Easily transported to the markets in buckets without water as long as the skin is kept moist, and it may survive in this condition for several days. ◆

Kissing gourami
Helostoma temminckii

FAMILY
Helostomatidae

TAXONOMY
Helostoma temminckii Cuvier, 1829, type locality not specified.

OTHER COMMON NAMES
French: Gourami embrasseur; German: Küssender Gurami; Spanish: Gurami besador, gurami besucón.

PHYSICAL CHARACTERISTICS
Length 9.8 in (25 cm). High body, laterally compressed. Head has large fleshy lips and several rows of spoon-shaped teeth unattached to the jaw bones. Wild-type coloration is greenish beige, with darker longitudinal lines along each scale row; a breed with uniform pink color is commonly cultivated in ponds. Adult fish has a highly specialized filter-feeding apparatus derived from modified gill rakers. Long dorsal fin with 16–18 spines and 13–16 soft rays; long anal fin with 13–15 spines and 17–19 soft rays.

Striking anatomical changes of the feeding system occur during development. Juveniles have normal conical teeth in jaws and on pharyngeal jaws. As the fishes mature, the jaw teeth are lost and substituted by a second type of spoon-shaped teeth in the fleshy lips. Lower pharyngeal jaws lose teeth completely, and their number is reduced in upper pharyngeal jaws, sitting on long bony bases so that the resulting structure resembles a brush.

DISTRIBUTION
Central Thailand, Malay Peninsula, Sumatra, Java, Borneo. Has been introduced to various countries as a food fish. Established populations in the Philippines, Sri Lanka, Bali, Colombia, and Florida, in the United States.

HABITAT
Occurs in sluggish streams, swamps, ponds, and lakes.

BEHAVIOR
Exhibits "kissing" behavior, in which they protrude their fleshy lips when grazing algae or during social encounters. They may also "kiss" during aggressive behavior or courtship individuals.

FEEDING ECOLOGY AND DIET
One of the most specialized filter-feeding teleosts, filters small (even unicellular) invertebrates and algae from the water. Also scrapes off algae and other *aufwuchs* (plants and animals adhering to parts of rooted aquatic plants and other open surfaces) from the substrate.

REPRODUCTIVE BIOLOGY
Exhibits typical spawning clasp. Several thousand small (0.04 in/1 mm) buoyant spherical eggs are released during one spawning phase that comprises numerous spawning bouts. Eggs with a large oil globule hatch after one day at 86°F (30°C). No parental care.

CONSERVATION STATUS
Not listed by the IUCN.

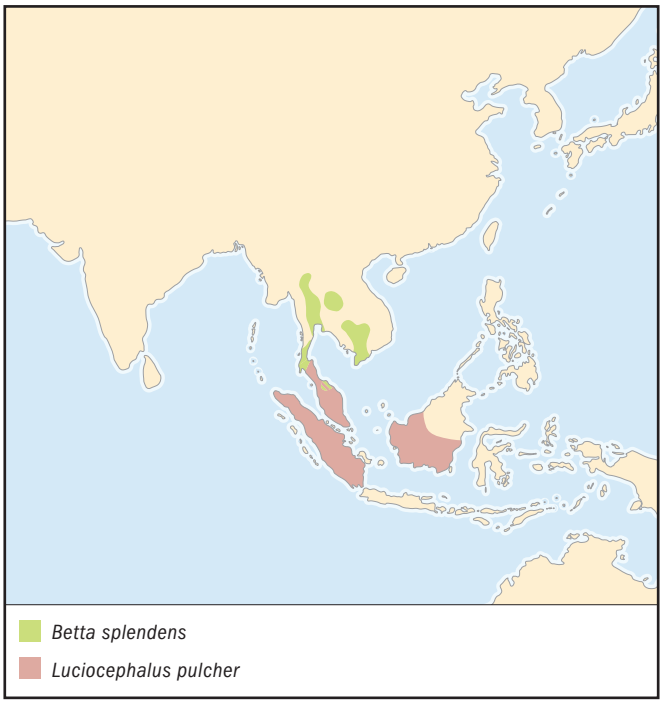
SIGNIFICANCE TO HUMANS
A valued food fish in Southeast Asia, and popular in the aquarium trade. ◆

Siamese fighting fish
Betta splendens

FAMILY
Osphronemidae

TAXONOMY
Betta splendens Regan, 1910, Menam River [= Mae Nam Chao Phraya], Thailand.

OTHER COMMON NAMES
English: Betta; French: Combatant, combattant du Siam; German: Siamesischer Kampffisch; Spanish: Combatiente siamés.



PHYSICAL CHARACTERISTICS
Up to 2.4 in (6 cm). Elongate cylindrical body, dorsal fin short with one to two spines and seven to 10 soft rays. Anal fin is long with two to five spines and 21–26 soft rays, caudal fin rounded. First soft ray of pelvic fin elongated. Sexually dimorphic; males have larger fins and a brighter coloration, females less conspicuously colored. Wild type with bluish body and blue and red fins. Two vertical iridescent marks on the opercle. Some breeds with greatly enlarged fins (sail fin) and different colors or combinations thereof, some almost completely red, blue, yellow, or black.

DISTRIBUTION
The original distributional range comprises the Chao Phraya basin in Thailand and northernmost Malay Peninsula (north of Isthmus of Kra). The species has been transported and released in various countries in Southeast Asia, and can now be found even in the Dominican Republic, Colombia, Brazil, and Florida, in the United States.

HABITAT
Tolerates a wide range of water parameters. Common in stagnant or standing water bodies with dense aquatic vegetation, especially in rice paddies and in canals. May dig into the mud when the water recedes and survive weeks in a small cocoon-like structure made of mud and probably mucus.

BEHAVIOR
This species is well known for its prominently developed aggressive behavior, especially against conspecific males. Confined to small tanks, males fight until one of them is killed. In Thailand, various breeds of *Betta splendens* are used in popular fighting matches in which people bet on the outcome.

FEEDING ECOLOGY AND DIET
Carnivorous, feeding mostly on small aquatic invertebrates, such as zooplankton and insect larvae.

REPRODUCTIVE BIOLOGY
The male constructs a bubble nest and aggressively defends the territory around it. Has typical spawning clasp. After the

spawning claps, male and female show spawning rigor, from which the male recovers earlier (after 4 s) than the female (after about 20 s). Up to 400 spherical eggs with a diameter of 0.04 in–0.05 in (1–1.4 mm) are laid per spawning sequence. They contain no oil globule and sink toward the bottom. While eggs are sinking they are collected by the male, later joined by the female, and stored in the nest. Hatching takes place after 32 to 35 hours at 84.2°F (29°C). Larvae swim free on the fourth day.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Very popular aquarium fish. Because of its hardy nature, often among the first species of freshwater fishes kept by beginners to the aquarium hobby. Of no interest to fisheries due to its small size. ◆

Pikehead
Luciocephalus pulcher

FAMILY
Osphronemidae

TAXONOMY
Diplopterus pulcher Gray, 1831, type locality not specified.

OTHER COMMON NAMES
German: Hechtkopf; Spanish: Cabeza de lucio.

PHYSICAL CHARACTERISTICS
Length 6 in (15 cm). Elongate, with large head and highly protrusible upper jaws. Labyrinth simple. Has separate endoskeletal ossification in front of basihyal, erroneously termed "gular element" by some authors. Caudal fin is rounded, dorsal fin is short with nine to 11 soft rays, anal fin with a median incisure and 18–19 soft rays, pelvic fin with filamentously elongate first soft ray extending to the end of the body. Color is light beige with longitudinal dark brown bands. There are several transverse stripes in the caudal fin that may be broken up into series of spots. A second, undescribed species from Sumatra and Borneo has numerous green iridescent spots along the body.

DISTRIBUTION
Malay Peninsula, Sumatra, and Borneo.

HABITAT
Smaller streams with acidic to highly acidic (down to a pH of 3.5) water; often caught among aquatic vegetation.

BEHAVIOR
The pikehead can protrude its upper jaw to about 33% of the head length, which is quite exceptional among teleosts. In captivity usually remains hidden among vegetation, from where it moves slowly toward prey. At a certain distance of around 3.9 in (10 cm), it makes a sudden rapid lunge (with a peak velocity of 150 cm/s^{-1} and a duration of 0.03 sec.) to surround the prey by protruding its upper jaws and expanding its huge mouth cavity. Suction seems to play only a minor role in capturing the prey.

FEEDING ECOLOGY AND DIET
Appears to feed exclusively on small fishes.

REPRODUCTIVE BIOLOGY
Mouth brooder with male parental care. Male defends territory around spawning site. Displays conspicuous sexually dichromatic coloration only during courtship and spawning. Mating with a reduced spawning clasp takes place at the bottom. All eggs are released during a single spawning bout, sink to the bottom, and are taken up into the male's mouth. The male mouth broods up to 150 eggs with a diameter of around 0.12 in (3 mm) for about four weeks. Eggs are pear-shaped, with a striking pattern of parallel surface ridges leading toward the micropyle (a preformed opening, the only place where sperm can enter the egg), where the ridges end in a counterclockwise spiral. This unique surface pattern also occurs in the genera *Parasphaerichthys*, *Ctenops*, and *Sphaerichthys*, demonstrating the close relationship of the four groups. Egg surface pattern may represent a sperm guiding device to enhance fertilization success. Upon release from the male's mouth, young pike-heads already measure 0.6 in (1.5 cm) long.

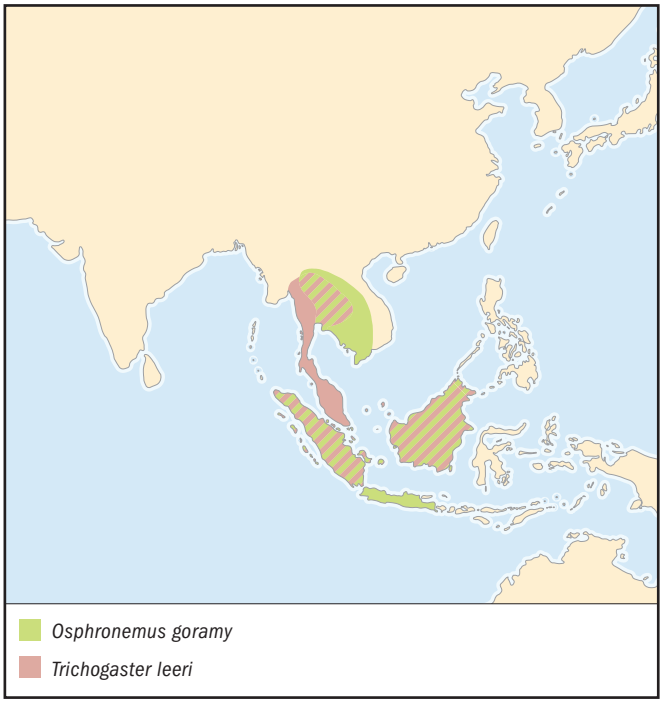
CONSERVATION STATUS
The species is not threatened or endangered, but may suffer in the future from habitat destruction.

SIGNIFICANCE TO HUMANS
Ornamental fish for specialized hobbyists. ◆

Giant gourami
Osphronemus goramy

FAMILY
Osphronemidae

TAXONOMY
Osphronemus goramy Lacepéde, 1801, Mauritius; China; Jakarta [Batavia], Java, Indonesia.



OTHER COMMON NAMES
French: Gourami géant; German: Riesengurami; Spanish: Gurami gigante, gurami comestible.

PHYSICAL CHARACTERISTICS
Largest species of anabantoids; up to 23.6 in (60 cm) and 19.8 lb (9 kg). High body, laterally compressed. Lateral line not interrupted and nearly straight. Dorsal fin has 11–14 spines and 12–14 soft rays. Anal fin has 10–11 spines and 20–23 soft rays. First soft ray of pelvic fin is very long, extending beyond caudal fin. Labyrinth highly complex in the adult, with the numerous folds supported by bony lamellae. Large males with prominent hump on the head. Juveniles have eight to 10 dark vertical bars and a conspicuous eyelike spot above the anal fin. Adults drab, grayish, olivaceous above and silvery or yellowish below in both sexes; no sexual dichromatism.

DISTRIBUTION
The species has been introduced in various areas outside of its natural range. Its original distribution probably comprised Thailand, the Malay Peninsula, Sumatra, Borneo, and Java. It now has established populations in India, Sri Lanka, Philippines, West Papua, Papua New Guinea, Madagascar, New Caledonia, and Colombia.

HABITAT
Occurs in swamps, lakes, and medium-to-large rivers. May also tolerate brackish water conditions.

BEHAVIOR
Nothing is known about the behavior of the giant gourami in the wild.

FEEDING ECOLOGY AND DIET
The giant gourami is omnivorous, feeding on plants, smaller vertebrates, invertebrates, and even dead animals.

REPRODUCTIVE BIOLOGY
Reaches maturity after the fourth year. The male builds a spherical to oval nest 11.8 in (30 cm) long, 7.9 in (20 cm) wide, and 3.9 in (10 cm) deep, which resembles a bird's nest, close to or below the water surface using mainly plant material. Nest building takes eight to 10 days. Eggs are deposited in the nest, and guarded by the male and female, and fanned through movements of the pectoral fins. The yellowish eggs are around 0.11 in (2.7 mm) in diameter and contain a large oil globule that makes them buoyant. Eggs may number more than 1,500 per nest. Hatching occurs after 10 days. Newly hatched fry measure 0.24–0.35 in (6–9 mm). Yolk sac is resorbed at around 15 days. After four months a length of 3.9 in (10 cm) may be reached.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A valued, common, and delicious food fish, eaten steamed, fried or baked. It has been introduced into more than 20 countries all over the world, and is important in aquaculture in tropical Asia. ◆

Pearl gourami
Trichogaster leeri

FAMILY
Osphronemidae

TAXONOMY
Trichopus leeri Bleeker, 1852, Sumatra.

OTHER COMMON NAMES
English: Diamond gourami, lace gourami, mosaic gourami; French: Gourami mosaïque, gourami perlé; German: Mosaikfadenfisch; Spanish: Gurami perla, Gurami mosáico.

PHYSICAL CHARACTERISTICS
Length 4.7 in (12 cm). Body laterally compressed with short dorsal fin of 5–7 fin spines and 8–10 soft rays; long anal fin with 12–14 spines and 25–30 soft rays. Pelvic fins with an extremely prolonged first soft ray behind the spine, followed by four short soft rays. This pelvic filament reaches up to two-thirds of the fish's total length, is highly movable in all three dimensions, and is used as an organ of taste because its surface is covered with numerous taste buds. A tactile function has also been demonstrated. Males can be distinguished from females by the posterior rays of the soft dorsal and soft anal fin being prolonged and projecting beyond the fin membrane. Coloration of the body consists of a grayish background, with numerous bright white spots all over the body and fins (hence the name "pearl" gourami), a black midlateral stripe that extends from the snout to the caudal peduncle, and a black spot at the base of the caudal fin. Males have bright nuptial coloration, especially when sexually active.

DISTRIBUTION
Freshwaters of Thailand, peninsular Malaysia, Sumatra, and Borneo.

HABITAT
Smaller or larger forest streams, usually with slightly acidic water.

BEHAVIOR
Nothing is known about the behavior of the pearl gourami in the wild.

FEEDING ECOLOGY AND DIET
No field data on gut contents is available, but judging from the small mouth and the numerous gill rakers, feeds on small aquatic invertebrates.

REPRODUCTIVE BIOLOGY
The onset of a reproductive period is characterized by an increasing aggressiveness of the male and the establishment of a breeding territory in which it builds a foam nest. Parts of aquatic vegetation or detritus may be incorporated into the foam mass. The foam nest is built from air gulped in at the surface and released as foam-coated bubbles below the nesting site, from either the mouth or the opercular cleft. The male's nuptial coloration is bright orange on the throat, pelvic filament, and anterior anal fin, with numerous bright white spots on the body and fins. Spawning takes place below the nest. The typical spawning clasp is performed. Eggs are usually released when the female's genital opening points to the nest. Up to 135 eggs are released during each bout of spawning, with up to 1,000 eggs per spawning sequence. A short phase (2–10 seconds) of spawning rigor follows egg release, during which the male and female remain motionless in their clasp. Eggs contain a large oil globule that renders them buoyant. Floating eggs are collected by the male and stored in the nest. Hatching occurs after 24 hours at 84.2°F (29°C). Free swimming is achieved after two to three days. The pearl gourami exhibits male parental care.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Consumed as a food fish and used in aquaculture. A common and popular aquarium fish. ◆

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Organizations

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Ralf Britz, PhD

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Channoidei
(Snakeheads)

Class Actinopterygii
Order Perciformes
Suborder Channoidei
Number of families 1

Photo: Snakehead fishes move along the ground using their fins at a fish farm in Singapore. They are popular in parts of Asia for medicinal benefits, are aggressive, and can live out of water for days. (Photo by Jonathan Searle/Reuters NewMedia inc./Corbis. Reproduced by permission.)

Evolution and systematics

The single-family (Channidae) suborder Channoidei (snakeheads) is composed of only two genera, *Channa*, which includes all Asian species, and *Parachanna*, which includes all African species. The two genera differ mainly in the morphology of the air-breathing (suprabranchial) organ; that of the latter being less developed. Currently, 25 species of *Channa* and three species of *Parachanna* have been recognized. Although snakeheads have been considered a sister group of the Anabantoidei (climbing gouramies) or the Synbranchiformes (swamp eels), the relationship of snakeheads to other fish groups still remains uncertain. The earliest fossil record of snakeheads is *Eochanna chorlakkiensis* from the Kuldana Formation, Pakistan (middle Eocene).

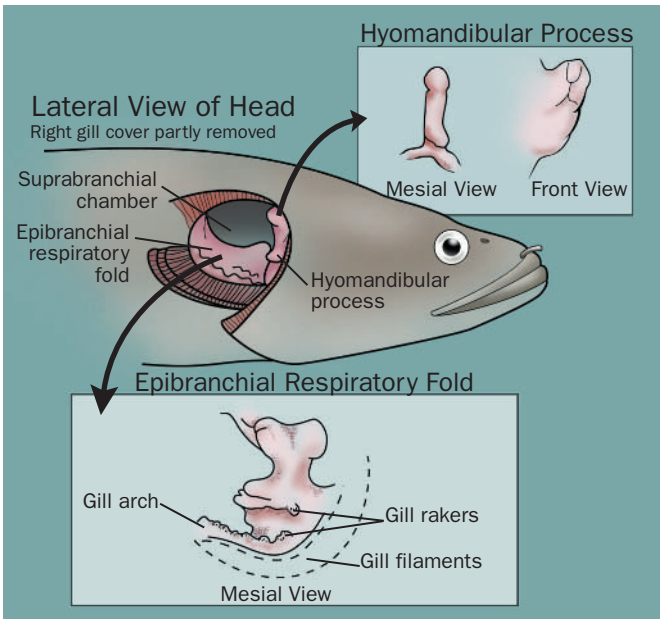
Physical characteristics

Snakeheads form a morphologically unique group of primarily freshwater fishes, which greatly vary in size at maturity. Some species have distinctively small pelvic fins, while a few others lack them completely. Generally, snakeheads have an elongated cylindrical body; flattened head; long, entirely soft-rayed dorsal and anal fins; a large mouth with well-developed teeth on both upper and lower jaws; tubelike anterior nostrils; a round to somewhat truncate caudal fin; cycloid or ctenoid body scales; shield-like scales on a head that superficially resemble that of a snake; a lengthy, elongated swim bladder reaching to the caudal peduncle region; and an accessory air-breathing apparatus (suprabranchial organ) in the head region. This suprabranchial organ is mainly composed of three parts: a suprabranchial chamber, epibranchial respiratory fold, and hyomandibular process.

Species of snakeheads can be distinguished based on coloration, meristics, and morphometrics, as well as the distribution of scales on the underside of the lower jaw, the shape of the head, and the morphology of the suprabranchial organs. Much taxonomic confusion has resulted from the fact that coloration in each species changes dramatically during growth, and in many cases, the color of juveniles is completely different from that of adults. One such case is the giant snakehead (*Channa micropeltes*), a popular aquarium fish that has striking black and red "racing stripes" as a juvenile, but variegated blackish markings as an adult. Many species have distinct adult coloration, such as ocellus (ocelli) on the body and/or caudal fin, vertical bands on the pectoral fins, and small spots on the body.

Distribution

Members of the genus *Channa* are widely distributed, occurring from Iran in the west, to China and southeastern Russia in the east, and throughout Southeast Asia, extending downward into the Philippines and Indonesia (Java being the southernmost location). Species of the genus *Parachanna* are restricted to central West Africa. Species are most diverse in tropical Asia. Some species are endemic to restricted areas that include special features such as tropical rainforests, such



Superbranchial chamber anatomy. (Illustration by Michelle Meneghini)

as the walking snakehead (*Channa orientalis*) from southern Sri Lanka, and the orange-spotted snakehead (*Channa aurantimaculata*) and rainbow snakehead (*Channa bleheri*) from northern Assam. Some species are now found outside their natural distributions, apparently as a result of human introduction. These include established populations of the northern snakehead (*Channa argus*) in Japan, the United States, and Aral Sea basin; the blotched snakehead (*Channa maculata*) in Japan; the bullseye snakehead (*Channa marulius*) in the United States; and the striped snakehead (*Channa striata*) in the islands of Indonesia east of Wallace's line, Papua New Guinea, New Caledonia, Fiji, Hawaii, Mauritius, and Madagascar. In Madagascar the striped snakehead has had a severely detrimental effect upon the island's endemic freshwater fish fauna.

Habitat

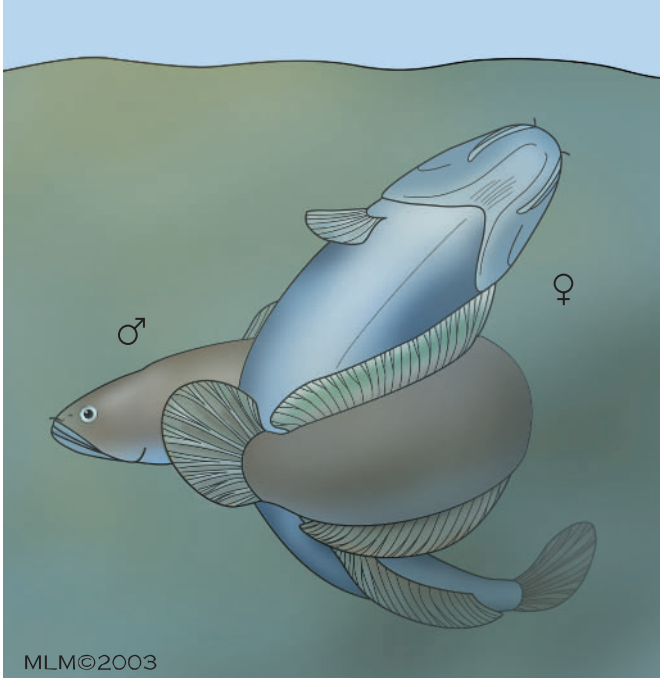
Most snakeheads prefer stagnant or slow-running waters, usually hiding under vegetation, rocks, and sunken trees. However, large species such as the northern snakehead, bullseye snakehead, and giant snakehead can usually be found inhabiting relatively deep waters with somewhat heavy vegetation in low, open country such as large rivers, swamps, ponds, and reservoirs. One species, the banka snakehead (*Channa bankanensis*), has been found only in peat swamps, which have dark brown, highly acid water. Most small species, such as the walking snakehead, usually live in mountain streams, but can also be found in lowland habitats. The northeastern Indian barca snakehead (*Channa barca*), a large species attaining 35.4 in (90 cm), is reported to live in holes within the banks of ponds and rivers. Many snakeheads are highly adaptable, being tolerant to a wide range of environments, including polluted waters.

Behavior

Highly territorial, snakeheads usually stay hidden, and migrate only short distances. Fry of some species have been reported to be cannibalistic, opportunistically eating eggs from a later spawn. Generally, the young tend to school. Snakeheads appear to need to breach the water surface periodically to exchange the air in their suprabranchial chamber. Experiments have shown that breathing surface air is far more important to them than using their gills. This is supported by evidence from the drowning deaths of fishes that have been caught in nets under water, and could not surface to breathe. Some species of snakeheads can live out of water for several days if their bodies are wet, amazingly migrating on land during the raining season by using their bodies, pectoral fins, and caudal fins. However, no one has reported them feeding while moving on land. The striped snakehead (*Channa striata*) has been reported to survive in the bottom mud of lakes, swamps, and canals that have dried up; fishermen using long knives to cut away the mud in layers have found these fishes singly or in clusters within cavities of the mud.

Feeding ecology and diet

Active during the day, although the dwarf snakehead (*Channa gachua*) has been reported to be nocturnal, all snakeheads are predatory, ambush feeders, eating almost any animal smaller than their mouths. Usually solitary feeders as adults, as juveniles they actively migrate in schools, hunting foods such as zooplankton, small insects, and crustaceans. Adult snakeheads feed on everything from insects (both terrestrial and aquatic) to young birds, including fishes, frogs, tadpoles, lizards, geckos, mice, rats, and ducks. They primar-



Mating posture of snakeheads. (Illustration by Michelle Meneghini)

ily hunt by sight, but smell and other senses may also be involved. They sometimes jump up from the water surface to grasp their prey.

Reproductive biology

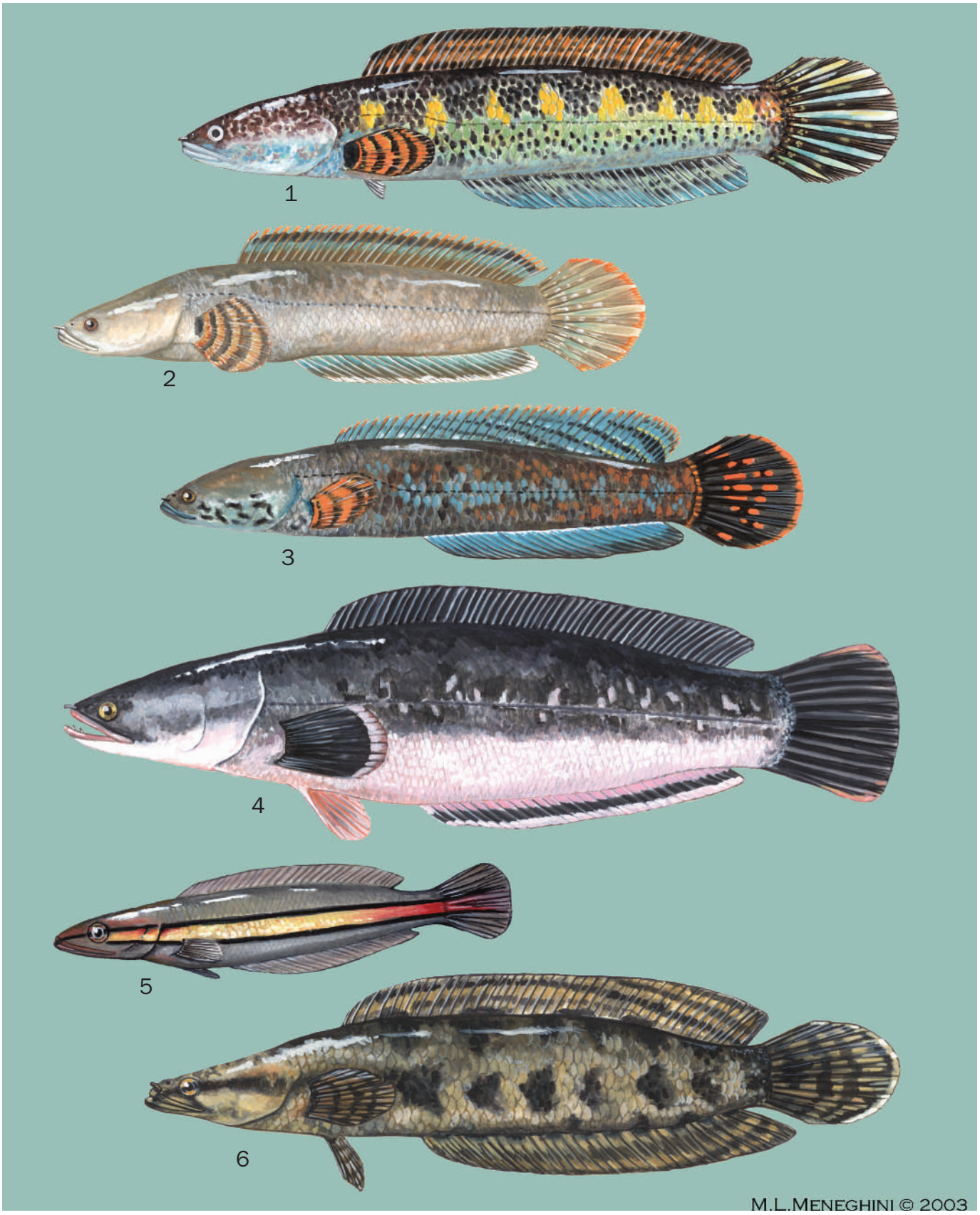
Although the reproductive biology of many species of snakeheads is still unknown, it does appear that they are monogamous, exhibit parental care, and become aggressive, especially so during breeding. Many are known to be nest breeders, the parents first clearing vegetation and then building a simple circular nest at the water surface. In these species, there is a spawning embrace with the male encircling the female, squeezing the eggs out, and fertilizing them. The eggs float upward into the nest, usually guarded. After hatching, the fry will be cared for by either parent, dependent on species. The giant snakehead, with its strong canine-like teeth, has been known to attack and seriously injure humans who disturb it, especially while guarding its brood. On the other hand, two small species, the walking and dwarf snakeheads, are known to be mouth brooders, with the male reported to keep the fertilized eggs, and later fry (for a few days), in his mouth.

Conservation status

Although generally not threatened, the status of populations of some species are poorly known. No species are included on the IUCN Red List.

Significance to humans

Most channid species are important food fishes in southern Asia and China and the flesh is considered delicious. Some medium-to-large species are cultured in ponds or in cages set in slow-running rivers. Although sold fresh and sun-dried, several species, northern snakehead (*C. argus*) and striped snakehead (*C. striata*), are known as intermediate hosts of parasites harmful to humans, including *Gnathostoma* (jaw worms), and should be cooked thoroughly at a high temperature before eating. Two species have even been used as predators to control tilapia in aquaculture ponds. Larger species are popular game fishes in Asia, and several species feature in local beliefs or myths. In October 2002, the U.S. Fish and Wildlife Service passed a rule that prohibits the importation of live snakeheads into the United States except by scientific, medical, or educational organizations, which would be required to obtain a permit to import the fishes.



1. Orange-spotted snakehead (*Channa aurantimaculata*); 2. Walking snakehead (*Channa orientalis*); 3. Rainbow snakehead (*Channa bleheri*); 4. Giant snakehead (*Channa micropeltes*); 5. Giant snakehead (*Channa micropeltes*) juvenile; 6. African snakehead (*Parachanna obscura*). (Illustration by Michelle Meneghini)

1. Striped snakehead (*Channa striata*); 2. Striped snakehead (*Channa striata*) juvenile; 3. Bullseye snakehead (*Channa marulius*); 4. Bullseye snakehead (*Channa marulius*) juvenile; 5. Ocellated snakehead (*Channa pleurophthalmus*); 6. Northern snakehead (*Channa argus*). (Illustration by Michelle Meneghini)

Species accounts

Northern snakehead
Channa argus

FAMILY
Channidae

TAXONOMY
Ophicephalus argus Cantor, 1842, Chusan Island, China.

OTHER COMMON NAMES
German: Amur-Schlangenkopf; Chinese: Hey yu; Japanese: Kamuruchi; Russian: Zmeegolov.

PHYSICAL CHARACTERISTICS
Length 44.1 in (112 cm); a large snakehead. Has relatively small scales (LL=61–72), no scales on the underside of the jaw, large canine-like teeth on the upper and lower jaws; two horizontal rows of 9–15 irregular dark brown blotches that sometimes coalesce, and brownish pectoral fins with a black mark at the base.

DISTRIBUTION
Central China (Yangtze to Luan River basins) including Korea to the Amur River basin, southern Russia; introduced and established in Japan, the United States, and republics in the former Soviet Union adjacent to Caspian Sea.

HABITAT
Lakes, swamps, marshes, reservoirs, and rivers in lowland slow-moving to stagnant temperate waters.

BEHAVIOR
Known to burrow into the mud and hibernate when the water becomes very cold, has not been reported to move over land.

FEEDING ECOLOGY AND DIET
Feeds on fishes, frogs, prawns, worms, crayfishes, and juvenile water birds.

REPRODUCTIVE BIOLOGY
Spawns usually in early morning from spring to summer, Male and female build donut-shaped nest about 39.4 in (100 cm) in diameter using aquatic plant debris. Female deposits an average of 7,300 eggs 0.06–0.08 in (0.15–0.2 cm) in diameter; incubation takes about 45 hours at 77°F (25°C). Guarded and cared for by the parents, newly hatched fry are all black, and leave the nest when they reach 0.03 in (0.8 cm), at which size the body has become yellowish.

CONSERVATION STATUS
Not threatened; common in almost all areas within its distribution.

SIGNIFICANCE TO HUMANS
One of the most popular food fishes in China, where it is believed to be beneficial for helping in postpartum recovery. ◆

Orange-spotted snakehead
Channa aurantimaculata

FAMILY
Channidae

TAXONOMY
Channa aurantimaculata Musikasinthorn, 2000, Dibrugarh, Assam, India.

OTHER COMMON NAMES
Assamese: Naga cheng.

PHYSICAL CHARACTERISTICS
Maximum length 19.7 in (50 cm). Has two large scales on each side of lower jaw undersurface, scales relatively large (LL= 51–54), black spot at the base of the pectoral fins with five vivid black vertical broad bands, and relatively small pelvic fins (less than half of pectoral fins). Very colorful, upper half of body dark brown to black, with seven or eight large irregular orange blotches, becoming yellow, golden, or orange below, and changing to blue ventrally, with many scattered small black spots.

DISTRIBUTION
Known only from Dibrugarh (Brahmaputra River basin), Northern Assam, India.

HABITAT
Streams, swamps, and ponds probably throughout the region's discontinuous patches of tropical rainforest.

BEHAVIOR
Effectively transverses wet terrestrial environments.

FEEDING ECOLOGY AND DIET
Nothing known.

REPRODUCTIVE BIOLOGY
Nothing known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Sold in local markets as food fish; also known as an aquarium fish. ◆

Rainbow snakehead
Channa bleheri

FAMILY
Channidae

TAXONOMY
Channa bleheri Vierke, 1991, upper portion of Dibru River, near Guijan, Brahmaputra River basin, northeastern Assam, India.

OTHER COMMON NAMES
Assamese: Deo cheng.

PHYSICAL CHARACTERISTICS
Length 3.9 in (10 cm), one of the smallest snakeheads. Has relatively large scales (LL= 42–46), no pelvic fins, and a single large scale on each side of the underside of the lower jaw. One of the most colorful snakeheads, has very distinctive 4–11 medium-to-large irregular red or orange spots on the caudal fin which sometimes coalesce; and pectoral fins with a black spot at the base and 7–9 black concentric bands.

DISTRIBUTION
Endemic to Brahmaputra River basin, northern Assam, India.

HABITAT
Forest streams, swamps, and ponds connected with the Brahmaputra River.

BEHAVIOR
Highly capable of terrestrial movement.

FEEDING ECOLOGY AND DIET
Nothing known, but is probably a predator feeding on insects, crustaceans, and small fishes.

REPRODUCTIVE BIOLOGY
The species guards the eggs, which float at the water surface.

CONSERVATION STATUS
Not threatened, but because of its relatively small, highly restricted distribution, along with its popularity among aquarists, there is a possibility that over-collecting of natural populations may cause a serious decline in the future.

SIGNIFICANCE TO HUMANS
Due to some spiritual reasons, not considered a food fish by the local Assam populace (the Assamese common name means "ghost [or spirit] snakehead"); a popular aquarium fish. ◆

Bullseye snakehead
Channa marulius

FAMILY
Channidae

TAXONOMY
Ophiocephalus marulius Hamilton, 1822, ponds and freshwater rivers of Bengal.

OTHER COMMON NAMES
English: Great snakehead; Thai: Pla chon ngu hao, pla kalon; Burmese: Nga yan dyne; Laotian: Pa gooan; Khmer: Trey raws; Bengali (West Bengal): Sal, gajal; Sinhalese: Ara.

PHYSICAL CHARACTERISTICS
Among the largest of snakeheads (48 in or 122 cm maximum length). It has 4–6 large round black blotches on the body; some populations have white margins and small white spots on these blotches. Also has a white or orange-rimmed ocellus on the upper portion of the caudal fin base (sometimes absent or indistinct in indiviuals over 300 mm SL), moderately large scales (LL=52–70), and no scales on the underside of the lower jaw. Also, young may have an orange longitudinal band running from the tip of the head to the caudal fin that fades as the fish matures.

DISTRIBUTION
Widely distributed in tropical Asia from the Indus River basin of Pakistan and the whole Indian subcontinent, including Sri Lanka, through Myanmar and Indochina. Also introduced and established in Florida, United States.

HABITAT
Large rivers, lakes, and reservoirs; prefers clear stretches of water with a sandy and rocky bottom.

FEEDING ECOLOGY AND DIET
Known to feed mainly on fishes. It probably also eats other vertebrates and invertebrates such as frogs and crustaceans.

BEHAVIOR
The species is capable of terrestrial movement.

REPRODUCTIVE BIOLOGY
In West Bengal this species spawns from April to June. Parents use their mouths to cut elaborate passages through the weeds leading to the floating bubble nest, where 2,000–40,000 light red-yellow eggs (0.08 in [2 mm] in diameter) hatch in about 54 hours. The pair also guards the fry.

CONSERVATION STATUS
Not threatened.

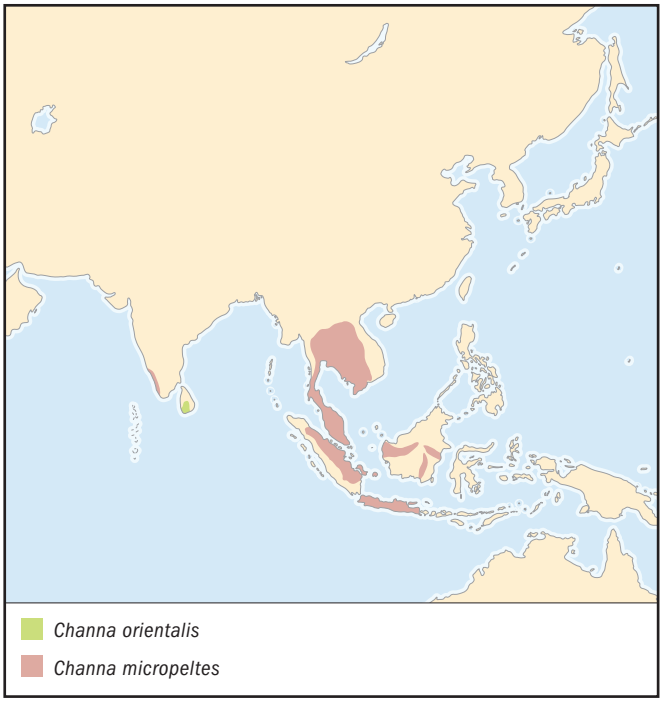
SIGNIFICANCE TO HUMANS
Readily seen as a food fish in India and some parts of Southeast Asia. A number of interesting local beliefs are attributed to this fish. In central Thailand, the common name means "cobra snakehead" and comes from the superstition that its bite is very poisonous, leading to death. In Myanmar, the Karen people regard it with awe and avoid eating it, practices that arise out the belief that these fish were formerly humans who were changed into fish for their sins, as well as the belief that if a person eats one, he or she will be transformed into a lion.

Giant snakehead
Channa micropeltes

FAMILY
Channidae

TAXONOMY
Ophicephalus micropeltes Cuvier in Cuvier and Valenciennes, 1831, Java.

OTHER COMMON NAMES
English: Red snakehead; Khmer: Trey chhdaur; Laotian: Pa do; Malay: Ikan toman: Thai: Pla chado; Vietnamese: Cá bong.



PHYSICAL CHARACTERISTICS
Length 51.2 in (130 cm); one of the largest snakeheads. Has very small scales (LL=83–106); patch of small scales near underside tip of lower jaw; large canine-like teeth on upper and lower jaws. Juveniles have vivid black horizontal stripe above and below a bright orange to red stripe running head to tail. Coloration fades into bluish black and white dappled upper body in adults.

DISTRIBUTION
Widely distributed in Southeast Asia (excluding Myanmar and northern Vietnam) and coastal region of southwestern India.

HABITAT
Large, slow-running to stagnant waters in open country.

BEHAVIOR
The most aggressive snakehead; has not been reported to travel over land.

FEEDING ECOLOGY AND DIET
Extremely voracious, consumes fishes of all kinds and sizes, frogs, and even juvenile ducks and water birds, killing far in excess of need. Young or subadults tend to school when hunting for smaller fishes.

REPRODUCTIVE BIOLOGY
Male and female build donut-shaped floating nest from surrounding aquatic vegetation into which the floating eggs are placed. Parents aggressively guard and care for eggs and fry. Once fry hatch, they soon form and forage as a dense school.

CONSERVATION STATUS
Relatively to very common in Southeast Asian range; status of population in southwestern India is unknown.

SIGNIFICANCE TO HUMANS
One of the most popularly marketed snakehead fishes in Southeast Asia. Adults are primarily game fish, juveniles are recognized worldwide as aquarium fish. ◆

Walking snakehead
Channa orientalis

FAMILY
Channidae

TAXONOMY
Channa orientalis Bloch and Schneider, 1801, India "orientali" (presumably Sri Lanka).

OTHER COMMON NAMES
English: Smooth-breasted snakehead; Sinhalese: Kola kanaya.

PHYSICAL CHARACTERISTICS
Maximum length 3.9 in (10 cm); one of the smallest snakeheads. Pelvic fins absent; body scales relatively large (LL=39–43), and a single large scale is on each side of the underside of lower jaw. Body often has bluish cast with 8–11 black descending bands on a grayish to dark brown dorsal background blending into a whitish ventral, with an orange to red outer margin on the dorsal, anal and caudal fins, a black spot at the base with 3–8 concentric black bands on the pectoral fins. Single orange or yellow-rimmed black ocellus at the back end of the dorsal fin in young usually fades away by maturity.

DISTRIBUTION
Endemic to tropical rainforest environment of southern Sri Lanka.

HABITAT
Small, shallow rivulets barely deeper than its body, and also in mountain streams, small ponds, and ditches.

BEHAVIOR
Known to effectively transverse land.

FEEDING ECOLOGY AND DIET
Feeds mostly on terrestrial and aquatic insects, caddisflies, and small fish.

REPRODUCTIVE BIOLOGY
Mouth brooders. Around 40 eggs are deposited in the floating nest, then 9–10 days after fertilization the male takes the eggs into his mouth for hatching. After hatching, either parent may hold the brood, which exits and enters through the gills, not the mouth. Fry feed on eggs laid later by their mother.

CONSERVATION STATUS
Not threatened, but a decline in the number of unpolluted streams and shrinking rainforests in Sri Lanka will probably affect future populations in the future.

SIGNIFICANCE TO HUMANS
A small number have been exported for the aquarium fish trade. ◆

Ocellated snakehead
Channa pleurophthalmus

FAMILY
Channidae

TAXONOMY
Ophicephalus pleurophthalmus Bleeker, 1851, Bandjermassing.

OTHER COMMON NAMES
Indonesian: Kerandang.

PHYSICAL CHARACTERISTICS
Total length 15.7 in (40 cm). Body is distinctively compressed laterally and quite deep compared to other snakeheads, has moderately large scales (LL= 49–55), large canine-like teeth on the upper and lower jaw, and patch of small scales near the tip of the underside of the lower jaw. Body grayish with scattered small black spots and several orange or orangey red-rimmed black ocelli, yellowish black to gray pectoral fins, and a single ocellus on the gill cover and middle of the caudal fin.

DISTRIBUTION
Islands of Sumatra and Borneo (western and southern portions), Indonesia.

HABITAT
Usually lowland, slow-moving murky rivers.

BEHAVIOR
Not known to be capable of terrestrial movement.

FEEDING ECOLOGY AND DIET
Nothing known; presumed to be a predator, feeding on fishes and other small aquatic animals.

REPRODUCTIVE BIOLOGY
Nothing known, but like other medium-to-large snakeheads, is probably a bubble nest builder.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Marketed as a food fish within its distribution, also quite popular as an aquarium fish. ◆

Striped snakehead
Channa striata

FAMILY
Channidae

TAXONOMY
Ophicephalus striatus Bloch, 1793, Tranquebar, Malabar coast, India.

OTHER COMMON NAMES
English: Chevron snakehead, snakehead murrel; German: Quergestreifter Schlangenkopf; Burmese: Nga-yan; Khmer: Trey raws; Bengali: Shol; Laotian: Pa kho; Malay: Aruan; Indonesian: Ikan gabus; Thai: Pla chon; Vietnamese: Cá lòk.

PHYSICAL CHARACTERISTICS
Length 23.6 in (60 cm). No scales on underside of the jaw, no large canine-like teeth on the upper jaw, moderately large scales (lateral line scales 50–61). Generally dark brown above, extending into irregular blackish bands below; no bands or spots on pectoral fins. Juveniles have black spot (sometimes forming an ocellus) at posterior end of dorsal fin, but this disappears as fish reaches maturity.

DISTRIBUTION
The most widely naturally distributed snakehead, occurs from Pakistan through Southeast Asia east to Yunnan, southern China. Has also been introduced and established in tropical islands, including Madagascar, Hawaii, New Guinea, the Philippines, and Sulawesi, Indonesia.

HABITAT
Tropical stagnant to slow-running lowland waters (prefers the former) with muddy bottoms, such as ponds, swamps, and ditches.

BEHAVIOR
Can move over land during rainy season. Reported to survive in cavities in the bottom mud of lakes, swamps, and canals that have dried up.

FEEDING ECOLOGY AND DIET
In native waters, feeds on smaller fishes, frogs, prawns, and worms.

REPRODUCTIVE BIOLOGY
Spawns year round, builds a nest in shallow (11.8–39.4 in/30–100 cm), swampy stagnant areas near waters' edge. Male and female use mouth and tail to clear away dense vegetation to make donut-shaped floating nest about 11.8 in (30 cm) in diameter, into which the translucent yellow nonadhesive eggs (about 0.06 in/0.15 cm in diameter) are placed. Hatching period lasts about three days, during which male guards the nest

until a short while after the vivid reddish orange fry hatch. After hatching, fry move in a dense school while foraging, still protected by male.

CONSERVATION STATUS
Not threatened; common in almost all areas within its distribution.

SIGNIFICANCE TO HUMANS
One of the most common and important freshwater food fishes in tropical Asia, also used for control of tilapia in pond aquaculture. In Myanmar, included in a spiritual ceremony to help a sick person recover. ◆

African snakehead
Parachanna obscura

FAMILY
Channidae

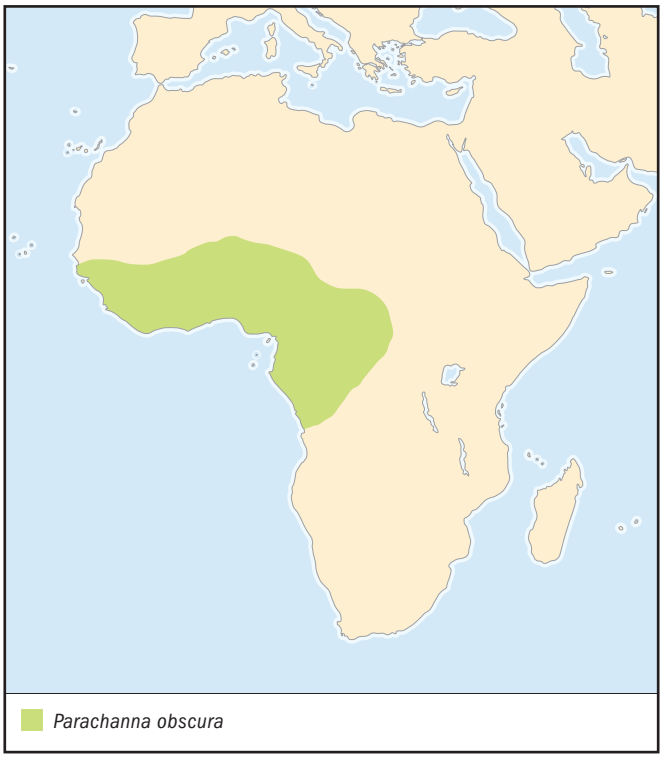
TAXONOMY
Ophiocephalus obscurus Günther, 1861, West Africa.

OTHER COMMON NAMES
German: Dunkelbäuchiger Schlangenkopf; Dinka: Abioth; Ga: Hauti; Hausa: Tuhi.

PHYSICAL CHARACTERISTICS
Length 15.7 in (40 cm). Medium-sized, head somewhat concave, pointed in lateral view and depressed anteriorly; has small scales (LL= 65–78), patch of small scales near the tip of the underside of the lower jaw, and no large canine-like teeth on the upper jaw. Body brown to dark brown with several large black blotches, blackish mark at base of pectoral fins along with several rows of black spots. Young have broad blackish band on body sides and light-edged ocellar spot at the caudal fin base.

DISTRIBUTION
The White Nile and from the Senegal and Chad Rivers to the Congo River basin in western Africa; most widely distributed African species.

HABITAT
Slow-running to stagnant waters, preferably with heavy vegetation, including rivers, streams, lakes, lagoons, and marshes.



BEHAVIOR
Adults are solitary ambush predators. Overland movement of this species has never been reported.

FEEDING ECOLOGY AND DIET
Juveniles feed on prawns, copepods, and aquatic insect larvae; adults prefer mostly fishes.

REPRODUCTIVE BIOLOGY
Female lays 2,000–3,000 eggs in October and November which are probably deposited in a nest and guarded by the male for 4–5 days after hatching.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Of minor importance as a food fish within its distribution, cultured in ponds and also used to control tilapia in aquaculture. ◆

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Prachya Musikasinthorn, PhD

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Pleuronectiformes
(Flatfishes)

Class Actinopterygii
Order Pleuronectiformes
Number of families Approximately 13

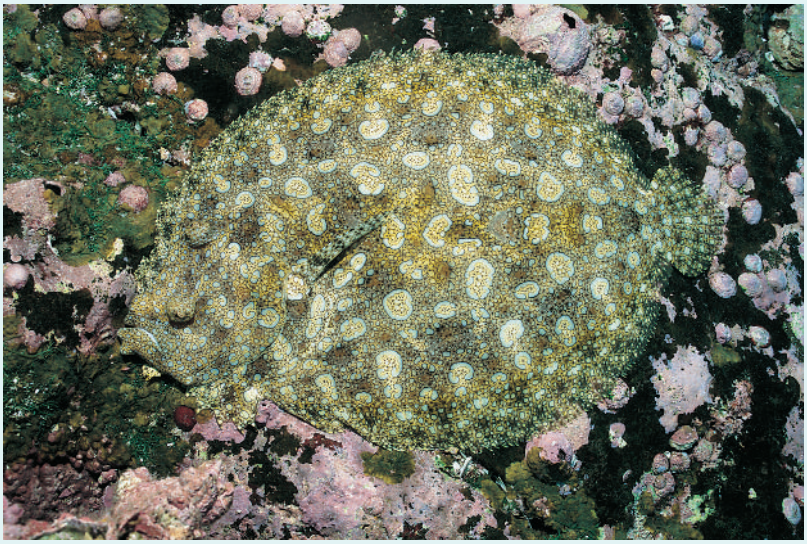


Photo: A Pacific leopard flounder (*Bothus leopardinus*) contrasting with the colorful sea ground near the Galápagos Islands. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

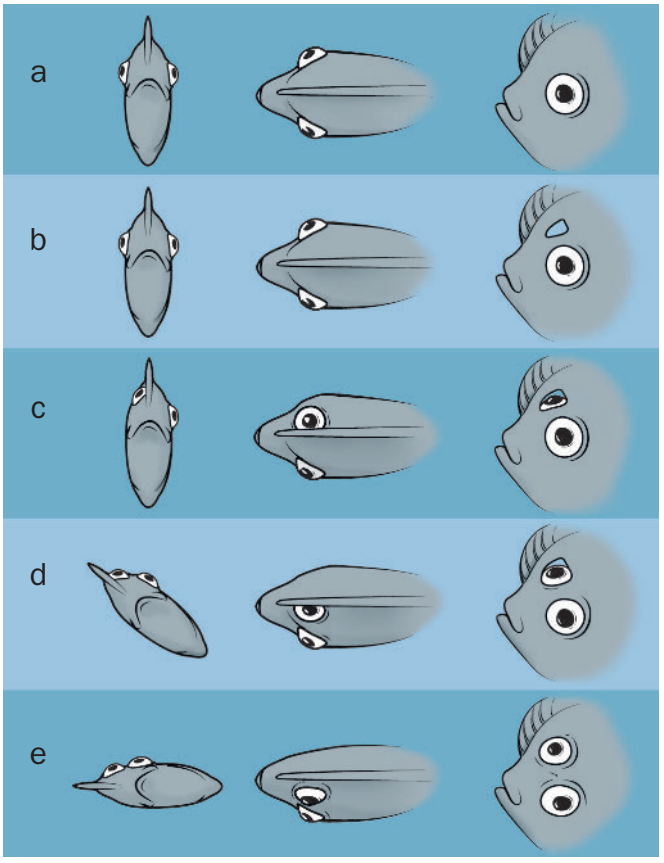
The flatfish body plan, with its spectacular morphological specializations, has had a long and successful presence among marine teleost fish assemblages dating back at least to the Tertiary, more than 50 million years ago (mya). The oldest flatfish fossils are otoliths dating from early Eocene times (53–57 mya). *Eobothus minimus*, a representative of the bothoid lineage with uncertain affinities within the group, is the oldest known skeleton representative of the Pleuronectiformes, dating at least to the Lutetian (some 45 mya) in the Eocene. The oldest soles, *Eobuglossus eocenicus* and *Turahbuglossus cuvillieri*, both known from single specimens from the Upper Lutetian (Eocene) of Egypt, are early flatfish fossils that appear nearly identical to skeletons of recent soleids. The earliest bothid and pleuronectid fossils also are surprisingly "modern-looking" species dating to the Eocene. The appearance of representatives of different flatfish families in fossil deposits dating to about the same time period indicates that diversification of many of the major lineages of flatfishes took place in the distant past, earlier than 45 mya. The nearly simultaneous appearance of flatfish fossils representing different lineages and encompassing nearly all of the structural features and diversity of the order also may indicate that diversification of these lineages occurred suddenly.

It also is evident from these early fossils that anatomical specializations of flatfishes, including asymmetry of the skull, supracranial extension of the dorsal fin, and modifications of the caudal skeleton, occurred earlier than the period to which these fossil flatfishes belong. When flatfishes evolved and how rapidly they diversified are unresolved questions. Flatfish fossils are unknown from true freshwater sediments, which may indicate that the ancestor of this group was a marine fish. Because fossil flatfishes are relatively rare, our knowledge concerning their evolutionary history is still very incomplete.

Flatfishes have unique morphological specializations related to their asymmetry. Although earlier hypotheses proposed that flatfishes share a common ancestor with some as yet unidentified perciform group of symmetrical fishes, the origin and sister group of flatfishes are unknown. Interrelationships among flatfishes are not well resolved, and work continues toward understanding the evolutionary relationships of these interesting fishes. The order Pleuronectiformes is monophyletic, based on the presence of three derived characters: the ontogenetic migration of one of the eyes; the anterior position of the dorsal fin origin (overlapping the cranium); and the presence of a recessus orbitalis, a muscular, sac-like evagination in the membranous wall of the orbit that can be filled with fluid, causing protrusion of the eyes to a higher position above the surface of the head (and above the bottom when the fish is buried).

Many groups of flatfishes that traditionally were recognized as families and subfamilies do not seem to represent monophyletic groups. The lack of detailed phylogenetic studies for several pleuronectoid groups hinders understanding of the interrelationships of flatfishes even at the family level. Ongoing research using both morphological and molecular approaches is expected to provide interesting results on such interrelationships of pleuronectiform taxa. Changes in our understanding of higher relationships among these fishes can be expected as additional information is discovered.

Two major lineages of flatfishes are recognized: the Psettoidei, made up of the family Psettodidae, and the Pleuronectoidei, containing all remaining flatfish groups. The Psettodids, or spiny-flounders, are a basal group of flatfishes hypothesized to be the sister group of the Pleuronectoidei. This suborder has one family with two species of *Psettodes*. These are relatively large flatfishes that do not feature strong



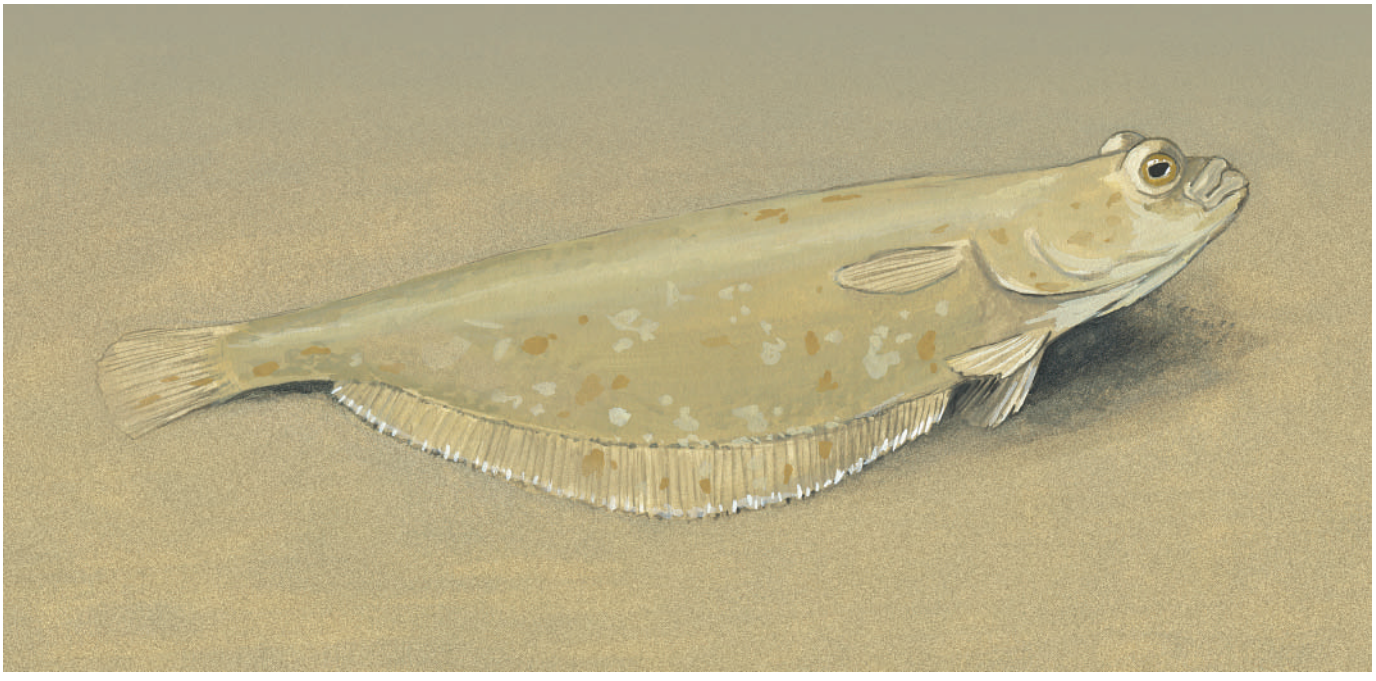
Developmental stages of eye migration in the larva from a symmetrical larva with an eye on each side of the head to the metamorphosed specimen with both eyes on same side of the head. (Illustration by Amanda Humphrey)

morphological asymmetries, as found in other flatfishes; there are both dextral and sinistral individuals in populations. These fishes are recognized easily by the posterior location of the dorsal fin, which does not advance onto the cranium anterior to the eyes; by spines in the dorsal and anal fins; by large mouths with specialized teeth; and by nearly rounded bodies without the obvious bilateral asymmetry in the lateral musculature that is evident in other flatfishes.

The Pleuronectoidei contains all of the more familiar flatfishes. At present, 13 families of pleuronectoid flatfishes are recognized, with *Tephrinectes* also representing a distinct lineage of uncertain status within the order. Phylogenetic relationships of some families and subfamilies and the monophyly of others (e.g., Paralichthyidae) are uncertain and in need of further study. Family groups within this suborder are the Citharidae, Scophthalmidae, Bothidae, Paralichthyidae, Pleuronectidae, Paralichthodidae, Poecilopsettidae, Rhombosoleidae, Achiropsettidae, Samaridae, Achiridae, Soleidae, and Cynoglossidae.

Physical characteristics

Flatfishes are deep-bodied, laterally compressed fishes that are easily and immediately recognizable anatomically, in that juveniles and adults (post-metamorphic individuals) have both eyes on the same side of the head. All flatfishes begin life as pelagic, bilaterally symmetrical fishes with an eye on each side of the head. During larval development, however, flatfishes undergo a spectacular ontogenetic metamorphosis, during which one eye migrates from one side of the head to the other, so that both eyes come to be present on the same side of the head. Depending upon the species, either the right or the left eye migrates. In relatively few species, eye migration is inde-



A pleuronectid flatfish with its anterior body raised off the substrate as it searches for prey. This posture represents a typical feeding behavior exhibited by benthic feeders among this important family of flatfishes. (Illustration by Amanda Humphrey)

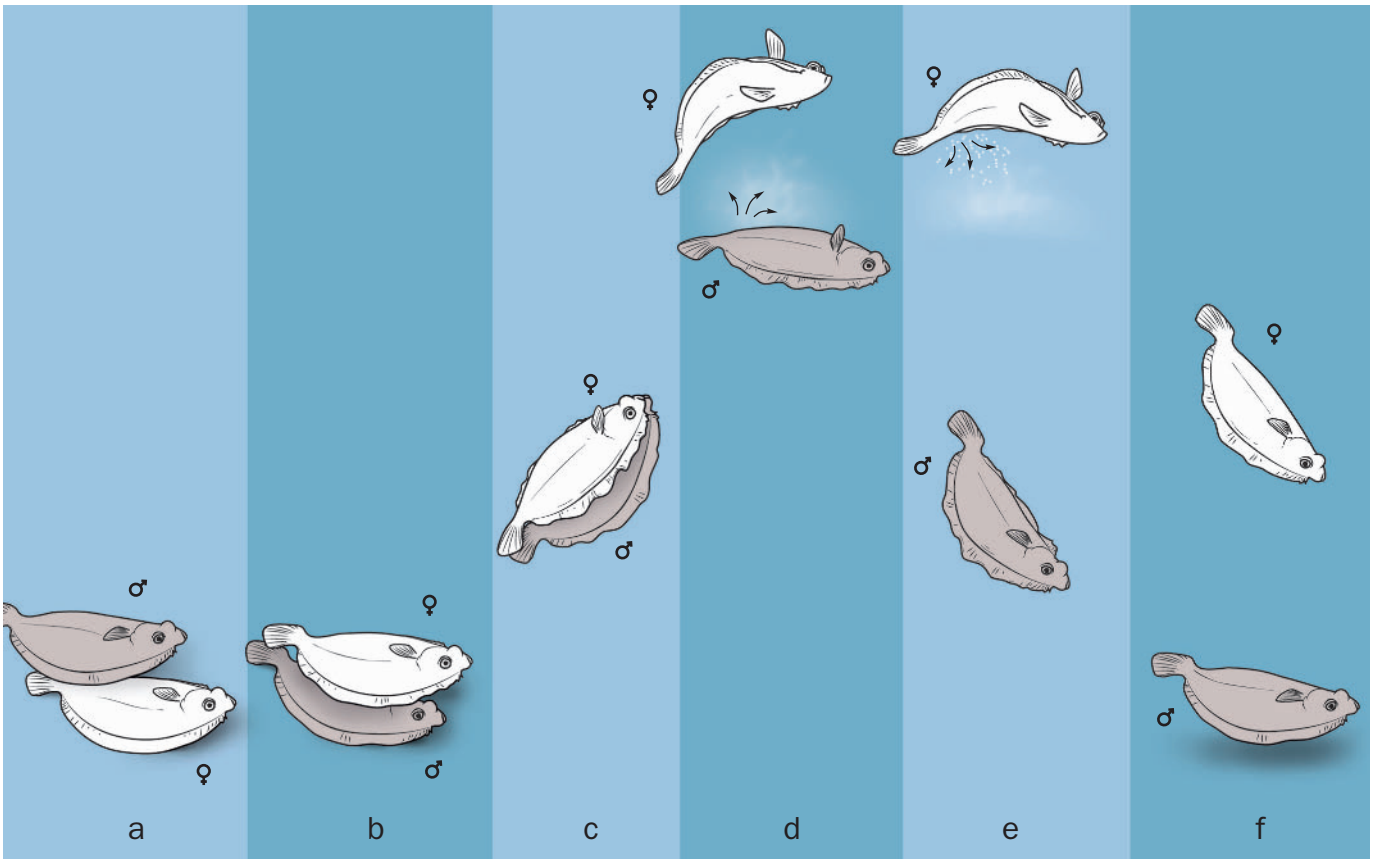


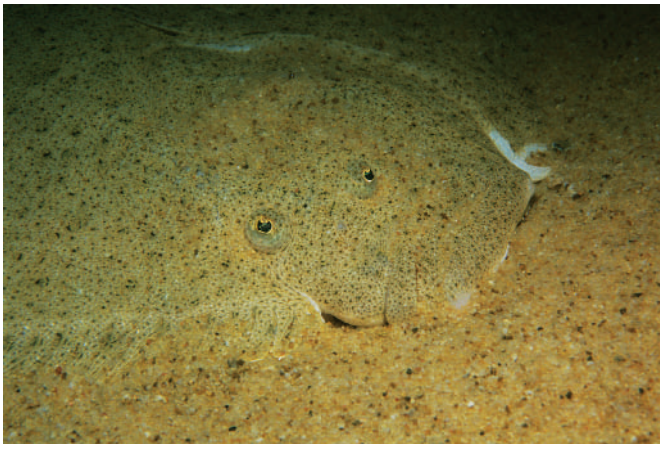
Illustration of mating of *Bothus ocellatus*. Short series of drawings reflecting the paired courtship swimming, rise off the bottom, and gamete release during reproductive events of this species. This is one of the best documented mating sequences observed for flatfishes. (Illustration by Amanda Humphrey)

terminate, but in most species eye migration is genetically fixed. The eyes may or may not come to lie in close proximity to each other when eye migration is completed.

Further deviations from a bilaterally symmetrical body plan occur in various external and internal structures, including placement of nostrils in the head, differential development of osteological features (especially bones in the anterior head skeleton), differences in jaw shape and dentition on either side of the body, degree of development of lateral body musculature, lateral line development and scale type on different sides of the body, differential coloration on ocular and blind sides, and differences in paired fin development on ocular and blind sides of the body. As a group, flatfishes are unique among fishes in their asymmetry, and they are noteworthy in that only they, among vertebrates, deviate so radically from a bilaterally symmetrical body plan.

Body shapes vary widely, ranging from nearly round, oval, and rhomboid to elongate and sometimes tapering to a sharp point. They may be either thick-bodied or thin-bodied, with or without a well-defined caudal peduncle. Flatfishes span a size range of about three orders of magnitude, from diminutive species, such as tonguefishes (*Symphurus*), which are sexually mature at a standard length (SL) of 0.98–1.6 in (2.5–4.0 cm), to giant species of halibuts (*Hippoglossus stenolepis* and *H. hippoglossus*), which reach nearly 6.6 ft (2 m) in total length and may weigh well over 661 lb (300 kg). Average total lengths of adults of most flatfish species are about 11.8 in (30 cm) or less.

Some flatfishes possess remarkable abilities to change the color and color patterns of their ocular surfaces to match the colors and patterns of the backgrounds on which they lie. Flatfishes typically exhibit distinct asymmetrical differences in pigmentation, with the ocular side of the head and body uniformly



A well camouflaged turbot fish (*Scophthalmus maximus*) on the sea bed. (Photo by Lawson Wood/Corbis. Reproduced by permission.)

A hogchoker (*Trinectes maculatus*) burying itself into the sand. (Photo by Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

whitish to dark brown or black, upon which there may be additional markings, such as ocelli, spots, crossbanding (complete and incomplete), or longitudinal or wavy stripes. Ocelli, spots, and crossbands may be fixed in number and position and may be useful for identification of some species. In species with strong asymmetrical coloration, the blind side of the head and body is conspicuously paler than the ocular side, typically uniformly whitish to pale yellowish. Flatfishes without strong asymmetrical pigmentation usually have blind sides that are darkly pigmented, sometimes as intensely pigmented as the ocular side; in others, although the blind sides are distinctly pigmented, they are less so than the ocular surface.

Except for the spiny flounders (Psettodidae), flatfishes typically lack spines in their fins. All of the fin rays are soft. Flatfishes have a single, long dorsal fin, whose origin is located in an anterior position overlapping the cranium. The single anal fin is also long and extends along most of the ventral side of the body from a point just behind the anus nearly to, or sometimes connecting to, the caudal fin. Most flatfishes typically have paired pectoral and pelvic fins, but in some groups these fins are reduced or lost. In addition, most flatfishes have a lateral line, at least on the ocular side, and most also have a lateral line on the blind side. Adult flatfishes also lack a swim bladder (though it is present in larvae).

Distribution

Species of flatfishes have nearly global occurrence in marine habitats, ranging from Arctic and boreal marine waters to Antarctic and southern waters. They are distributed broadly throughout the world's temperate marine zones and are especially speciose in marine habitats in tropical regions. Within all regions, flatfishes are most diverse where extensive continental shelves with complex habitats are located in shallow water. The widest diversity of flatfish species occurs in the Indo-West Pacific region.

Habitat

Flatfishes occur nearly globally in marine habitats and occupy diverse bathymetric environments, ranging from shallow-water to deep-water habitats to about 6,560 ft (2,000 m). Relatively few species inhabit freshwater environments. The greatest diversity of flatfishes, about 74% of the known species, is found in habitats ranging from near shore to depths of about 328 ft (100 m) on the continental shelf.

The majority of flatfishes occur in shallow marine waters, in coastal areas and estuaries, and on the inner continental shelf, where there are soft-sediment bottom types. Flatfishes also occur on a variety of sediments on the outer continental shelf and upper continental slope. Flatfishes can be found on intertidal flats following the tide line to deeper habitats. In tropical waters, flatfishes inhabit shallow mangrove estuaries and adjacent mud flats, sea grass beds, and mud bottoms along the coast. Within reef-associated habitats, which are distributed widely across tropical oceans, flatfishes are found on reef flats, on back-reef slope areas and in lagoons associated with reefs, and around coral outcrops, as well as on sandy substrates interspersed around reef spurs. Flatfishes inhabit various sediments, including silt, mud, sand, and sand-shell mixtures, with some species also occurring on rocky or pebbly bottoms.

Behavior

Flatfishes generally lie on the bottom on their blind side. They can be found either on top of the sediments or partially buried under a fine layer of sand or silt with only their eyes protruding above the sediments. Many flatfishes are stationary for long periods of time. When swimming above the bottom, they use a "pleuronectiform" swimming mode, in which waves of muscle contraction are passed along the body, beginning in the anterior region and continuing posteriorly. Most species can utilize a more rapid escape response, where the caudal fin is brought into play, creating a powerful and speedy swimming response.

Surprisingly little is known concerning the social organization of most flatfish species. Flatfishes are non-schooling species; many occur as solitary individuals, but a few and perhaps many individuals may congregate in a general area. Males of some species may display aggressive behavior to one another during the mating season. The majority of flatfish species are diurnally active. Some species are active throughout the daytime, whereas others have peak activity at or around sunrise and sunset. Nocturnal activity is a major adaptation evident in the Soleidae, Achiridae, and Cynoglossidae.

Extensive migration patterns have been well documented for some commercially important species of northern temperate flatfishes, such as the plaice, summer flounder, and halibuts. For most flatfishes, in particular the many tropical species, little is known concerning their movements or migrations. Small, reef-associated species probably have limited home ranges and do not engage in any seasonal migrations.

Feeding ecology and diet

Flatfishes are extremely successful in conducting life on or near the bottom, where they function in pivotal ecological roles as both predator and prey. Flatfish diets include such prey as shrimps, decapod and other crustaceans, mollusks,

polychaetes, and many other types of small invertebrates, as well as echinoderms, fishes, and cephalopods. Small-mouthed species, especially tonguefishes (Cynoglossidae), achirid soles (Achiridae), and true soles (Soleidae), feed on a broad spectrum of smaller epifaunal and infaunal organisms.

Halibuts, larger species of bothid and paralichthyid flounders, larger pleuronectids, and the larger scophthalmids are active predators that consume fishes, larger and more active crustaceans (shrimps, lobsters, crabs), and cephalopods (squids and octopuses). The halibuts, with their great size and swimming abilities, actively pursue and chase down their prey, whereas other large flatfishes generally are ambush predators that lie on the bottom or partially buried within the sediment, concealed by their camouflage coloration and awaiting unsuspecting prey to approach within striking distance.

All life stages of flatfishes are eaten by predators that include both invertebrates and vertebrates. While in the plankton, eggs and larvae are consumed by jellyfishes, ctenophores, arrow worms, mysid shrimps, and fishes. Young, newly settled flatfishes are attacked and consumed by crabs, shrimps, and fishes. Juvenile and adult flatfishes fall prey to a wide variety of predatory fishes, including cods, hakes, sculpins, rockfishes, striped bass, other flatfishes (sometimes their own species), monkfish, bluefish, cobia, groupers, moray eels, sea ravens, large skates, stingrays, and various sharks, as well as birds (egrets, herons, cormorants, gulls), seals, and sea lions.

Reproductive biology

The reproductive behavior of most flatfishes is not known. Direct observations of courtship and mating have not been made for the majority of flatfish species. The sexes are separate, and individuals usually do not change sex during their lifetimes. Flatfishes have external fertilization. Where reproductive behavior has been observed, individual males and females may pair up during courtship and spawning. Sometimes the mating pair is joined by other males.

Most flatfishes spawn planktonic eggs that float freely in the water column. Some pleuronectid flatfishes, such as the winter flounder, lay eggs that are demersal and adhesive, such that after the female releases them, they remain on the bottom and stick to each other and to other items. Even among species with demersal, adhesive eggs, flatfishes do not construct nests during spawning, nor do they exhibit any type of parental care. Upon hatching, flatfish larvae are planktonic and usually are found in the water column far above the bottom. Larval stages vary in duration from a few days to a couple of months; the duration of larval stages is influenced greatly by ambient water temperatures. Following eye migration and metamorphosis, young flatfish settle out of the water column and assume a benthic lifestyle, with many species utilizing shallow-water habitats as nursery areas.

A strong seasonality in reproductive period has been noted for most temperate and boreal flatfishes, with most species having one spawning season per year. The timing of spawning seasons within the year varies by species and also by latitude. Some species spawn during periods of seasonally high temperatures, whereas others spawn during wintertime. Some warm temperate species may have two spawning periods per year; for tropical and subtropical species, spawning periods may extend over several months. Spawning among temperate marine species corresponds to annual productivity cycles that are related to temperatures and photoperiods. In some tropical regions, spawning by some flatfishes also seems to correspond to seasonal monsoons, which influence productivity cycles.

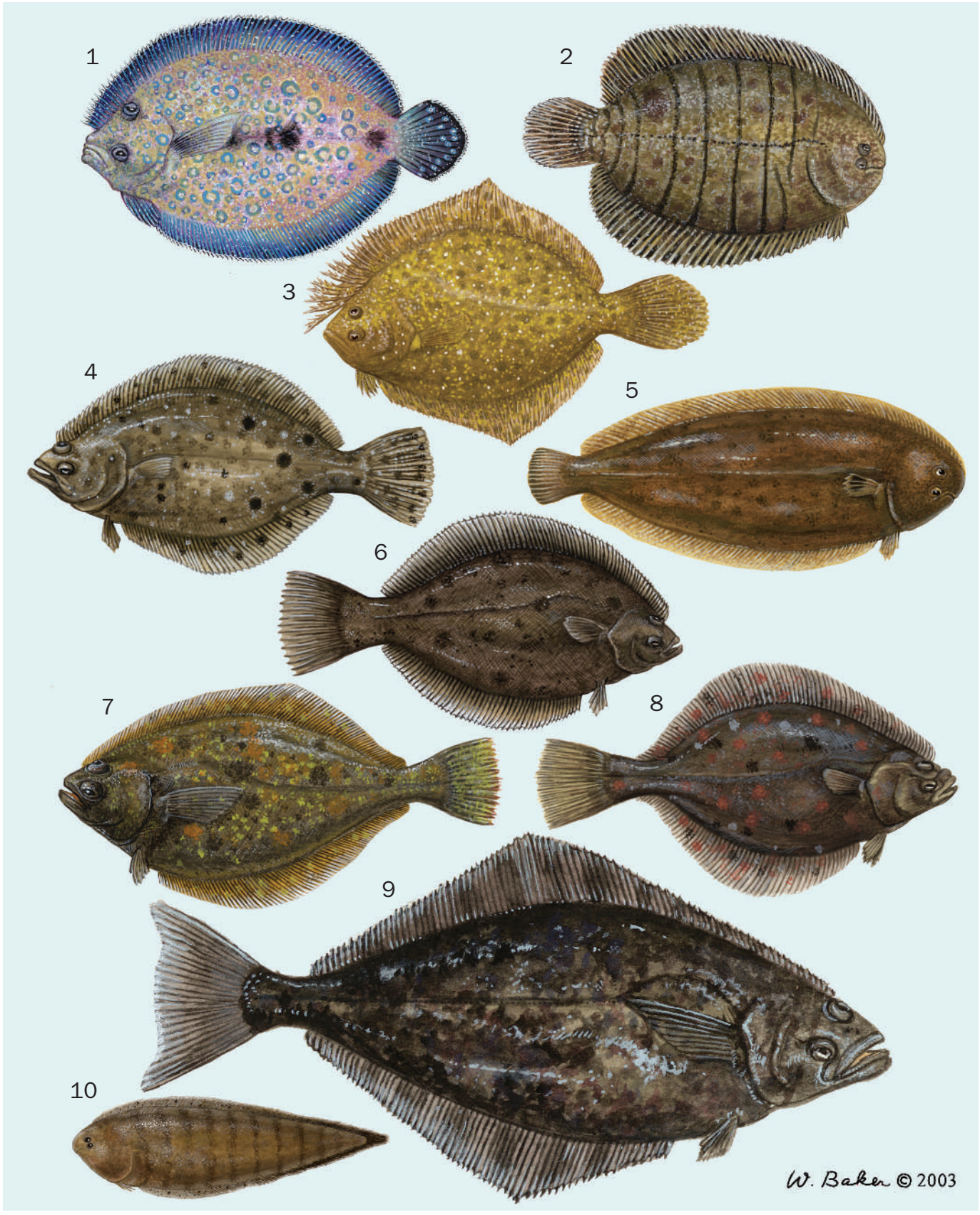
Close-up of the yellowtail flounder (*Limanda ferruginea*). (Photo by Jeffrey L. Rotman/Corbis. Reproduced by permission.)

Conservation status

Two pleuronectids are cited by the IUCN—the Atlantic halibut, which is listed as Endangered, and the yellowtail flounder, which is listed as Vulnerable. Overfishing is primarily responsible for reductions in many flatfish populations, especially for large, commercially important species. Throughout the world, stocks of commercially important flatfishes are considered to be fully exploited—for many, even overexploited. Other factors contributing to reductions in populations of flatfishes include habitat destruction and pollution, especially serious situations for flatfishes that utilize estuaries and other coastal habitats, such as sea grass meadows and mangrove forests, as nursery habitats.

Significance to humans

Flatfishes are an important group of food fishes. Medium-size and large species of most families are consumed wherever they are captured, and in some regions even the smallest flatfishes also are sold as food for people. In such regions as the North Atlantic and North Pacific Oceans and also in Southern Hemisphere regions, such as Australia, New Zealand, and South America, flatfish populations are sufficiently large to constitute major fishery resources. Some of the smaller flatfishes, especially those taken as by-catch in shrimp trawl fisheries (tonguefishes, soleids, achirids, bothids, and paralichthyids), are considered to be a nuisance by fishermen because they so firmly entangle themselves in the nets that they cannot easily be shaken out. Clearing the nets after heavy catches of these flatfishes, especially tonguefishes, soleids, and achirids, requires manually extracting fishes from the nets, a time-consuming task.



1. Peacock flounder (*Bothus lunatus*); 2. Hogchoker (*Trinectes maculatus*); 3. Windowpane flounder (*Scophthalmus aquosus*); 4. Summer flounder (*Paralichthys dentatus*); 5. Common sole (*Solea solea*); 6. Winter flounder (*Pseudopleuronectes americanus*); 7. Pacific sanddab (*Citharichthys sordidus*); 8. Plaice (*Pleuronectes platessa*); 9. Pacific halibut (*Hippoglossus stenolepis*); 10. California tonguefish (*Symphurus atricaudus*). (Illustration by Wendy Baker)

Species accounts

Hogchoker
Trinectes maculatus

FAMILY
Achiridae

TAXONOMY
Pleuronectes maculatus Bloch and Schneider, 1801, Tranquebar, India (in error).

OTHER COMMON NAMES
French: Sole bavoche; German: Amerikanische Seezunge.

PHYSICAL CHARACTERISTICS
Small, oval, dextral flatfish that have a deep and thick body without a definite caudal peduncle. The dorsal and anal fins are free from the caudal fin, and the right pelvic fin is joined to the anal fin. A relatively small head, with the snout slightly overhanging the small, subterminal mouth. The eyes are small, flat, and separated by a small space. The dorsal fin originates at the tip of the snout. No pectoral fins. The lateral line is straight. The skin is very slimy with mucus. Scales are ctenoid and very rough on both sides of the body. The ocular side is slate-olive to dark brown, with numerous conspicuous, darker transverse crossbands. There is also a longitudinal stripe along the midregion and, occasionally, a number of darker, diffuse blotches scattered over the surface. The blind side is dirty white; some specimens have numerous irregularly rounded spots, varying in both size and number, scattered over the blind side. This species reaches lengths of about 7.9 in (20 cm), with most averaging about 2.4–5.9 in (6–15 cm). They live for about seven years. Females grow larger and live longer than males.

DISTRIBUTION
Western North Atlantic in marine, estuarine, and freshwaters along the Atlantic coast of North America from Maine to the Gulf of Mexico.

HABITAT
They occur most commonly on mud, sand, or silt bottoms in coastal bays and estuaries with brackish water. In larger estuaries, young (small) fish tend to be found in upper reaches of estuaries, sometimes at considerable distances upstream into freshwater portions of coastal rivers. Fish size generally increases with increasing distances down estuary. The largest hogchokers usually are found in the lower estuary and also on the inner continental shelf to about 82 ft (25 m) and rarely to about 246 ft (75 m). Able to withstand a considerable range of temperatures of about 34–95.2°F (1.1–35.1°C). Euryhaline (able to withstand a range of salinities), ranging in salinity from freshwater to about 50 ppt. Can tolerate low oxygen conditions for periods up to 10 days. Will move out of areas with extremely low oxygen levels.

BEHAVIOR
Under laboratory conditions, hogchokers were active only during the dark period, with peak activities associated with times of slack tide in the natural habitat. Under continuous dim light, activity peaks coincided with slack tide, and fish were active in the diurnal as well as the nocturnal phase of the cycle.

FEEDING ECOLOGY AND DIET
Opportunistic, nocturnal feeders that eat a variety of small invertebrate prey, including amphipods, clam siphons, annelid worms, copepods, and small fishes. These fishes tend to macerate their food. Hogchokers are consumed by a variety of predators, including bull sharks, sandbar sharks, smooth dogfish, stingrays, striped bass, weakfish, bluefish, and cobia.

REPRODUCTIVE BIOLOGY
Mature at two to four years old and at sizes as small as about 2 in (5 cm). Probably a serial spawner. Annual fecundity has not been estimated for this species. Batch fecundity varies with fish size. Small females, about 3.5 in (9 cm), produce about 11,000 eggs, and larger females, 4.3–6.3 in SL (11–16 cm SL), produce from 23,000 to 54,000 eggs. The spawning season is April to October, but eggs have been reported as early as January, and in the southern Gulf of Mexico spawning may occur year-round. Spawning takes place in estuaries between 6 P.M. and 10 P.M., when water temperatures reach 68–77°F (20–25°C). Hogchoker eggs are pelagic in high-salinity waters and demersal in lower-salinity waters. Hatching occurs about one to two days after spawning. Eye migration begins at about 0.2 in (5 mm), 34 days after hatching, and is completed when fish are about 0.7 in (18 mm).

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Edible but noncommercial species of no interest to fisheries, owing to their small size. They sometimes are captured and sold to hobbyists in the aquarium fish trade. ◆

Peacock flounder
Bothus lunatus

FAMILY
Bothidae

TAXONOMY
Pleuronectes lunatus Linnaeus, 1758, Bahamas.

OTHER COMMON NAMES
French: Rombou lune; Spanish: Lenguado ocelado.

PHYSICAL CHARACTERISTICS
Sinistral flatfish with an oval and moderately deep body. Rounded to bluntly pointed caudal fin. The dorsal profile of the snout has a distinct notch above the nostrils, and there is a stout spine on the snout of adult males (a bony knob in females). Eyes are relatively large, with the lower eye distinctly anterior to the upper and with a broad interorbital space that is conspicuously wider in males. The moderately large and oblique mouth extends slightly beyond a vertical line through the anterior margin of the lower eye. Jaws have an irregular double row of small teeth. Ocular side upper pectoral fin rays are conspicuously elongate in males. Scales are ctenoid on the ocular side and cycloid on the blind side. The lateral line has a steep arch above the pectoral fin. Ocular side is grayish brown,

with numerous bright blue rings and rosettes covering the entire ocular side and with two to three large blackish spots on the straight portion of the lateral line. Larger individuals also have dark transverse bands on the ocular side pectoral fin. Maximum lengths to about 17.7 in (45 cm), with most individuals about 13.8 in (35 cm) long.

DISTRIBUTION
Marine coastal waters of the tropical and subtropical western Atlantic, including Bermuda, the Bahamas, Florida, throughout the Caribbean, and south to Fernando de Noronha, Brazil.

HABITAT
Shallow waters from the shore to about 213 ft (65 m). Found chiefly on sandy bottoms, often within or near coral reefs, and also in sea grass and mangrove habitats.

BEHAVIOR
Diurnally active. Often observed resting on the sandy bottom, sometimes partially buried in the sand. Occasional specimens are also observed resting on top of small coral reef tops. When swimming, they glide along just above the bottom using wave-like motions. Peacock flounder can change colors rapidly to blend in with the background.

FEEDING ECOLOGY AND DIET
Visually feeding, ambush predator that eats primarily small fishes but also consumes crustaceans and octopuses. They often lie in wait on sand patches adjacent to reef areas to intercept small fishes undertaking crepuscular migrations between reef and sea grass habitats. Lizard fishes, snappers, groupers, and various sharks and stingrays eat peacock flounders.

REPRODUCTIVE BIOLOGY
Off Bonaire in December, peacock flounder spawning took place just before sunset, with elaborate spawning behavior observed for mating pairs. Males and females would approach each other with pectoral fins held erect to initiate courtship activity. The male, with its ocular side pectoral fin held erect, first paralleled the female as they swam above the substrate. The male then positioned himself underneath the female; with their snouts touching and the male's body arched backward, the pair began a slow rise (about 15 seconds) of about 6.6 ft (2 m) off the bottom, when they simultaneously released their gametes and rapidly returned to the bottom.

CONSERVATION STATUS
Probably not threatened, but population status is unknown throughout most of its distribution. Because of its size and food qualities, this species could be susceptible to local overfishing.

SIGNIFICANCE TO HUMANS
Peacock flounder are caught incidentally in artisanal fisheries throughout their range. ◆

California tonguefish
Symphurus atricaudus

FAMILY
Cynoglossidae

TAXONOMY
Aphoristia atricauda Jordan and Gilbert, 1880, San Diego Bay, California.

OTHER COMMON NAMES
French: Langue californienne; Spanish: Lengua de perra.

PHYSICAL CHARACTERISTICS
Small, sinistral flatfish with the characteristic tonguefish teardrop-shaped body terminating posteriorly in a point without a distinct caudal fin. The small head has a pointed snout. The small eyes are set close together. A small, subterminal mouth

with small teeth best developed on the jaws of the blind side. Dorsal and anal fins are conjoined with the caudal fin, forming one continuous fin around nearly the entire body. Lacks a lateral line on either side of the body, lacks pectoral fins in adults, and has a pelvic fin only on the ocular side. Ocular side is uniformly medium to dark brown, with a series of complete or incomplete darker crossbands and with the posterior fifth of the body much darker than the anterior regions. Blind side is uniformly whitish or yellowish. Reach lengths to about 8.3 in (21 cm), but most are smaller, usually averaging only about 5 in (13 cm). Little is known concerning longevity, growth rates, or population structure of this species.

DISTRIBUTION
Inner continental shelf of the eastern Pacific from Washington to the Pacific side of Baja California Sur and along the western shore of Sonora and Sinaloa, Mexico.

HABITAT
Sand or mud bottoms at depths ranging from 9.8 to 328 ft (3–100 m), with most adults taken between 98.4 and 262.5 ft (30–80 m). Juveniles tend to inhabit shallower waters than do adults.

BEHAVIOR
Little is known. Probably nocturnally active and also active at other periods of low-light levels. During the daytime it remains partially or totally buried in the sediment, except for the anterior head region.

FEEDING ECOLOGY AND DIET
Consume a variety of small benthic invertebrates, including harpacticoid copepods, amphipods, ostracods, nematodes, small bivalve mollusks, and polychaetes. Predators of California tonguefish include sharks, electric rays, stingrays, and various bony fishes.

REPRODUCTIVE BIOLOGY
Little is known. They spawn planktonic eggs from June to September; larvae hatch at about 0.08 in (2 mm). Larvae transform between 0.7 and 1 in (19 and 25 mm) in length and settle to the bottom during late fall and winter. Probably a serial spawner, producing several batches of eggs during a protracted spawning season.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Of little commercial value, owing to its small size. ◆

Pacific sanddab
Citharichthys sordidus

FAMILY
Paralichthyidae

TAXONOMY
Psettichthys sordidus Girard, 1854, San Francisco, California.

OTHER COMMON NAMES
English: Mottled sanddab, soft flounder, melgrim; Spanish: Lenguado arenero del Pacifico, lenguado.

PHYSICAL CHARACTERISTICS
Medium-sized, sinistral flatfishes with an elongate to oval body; large head with large terminal mouth; and slightly rounded, almost square caudal fin. Eyes are large, with the lower eye in advance of the upper eye and separated from it by a sharp, naked bony ridge. Pectoral fins are large and pointed. Lateral line is nearly straight. Scales are ctenoid on the ocular side of the body and cycloid on the blind side. Ocular side is a dull light brown, mottled with brown or black and sometimes yellow to orange speckles or white spots. Blind side is off-white to tan. Maximum lengths of about 16.1 in (41 cm) and weights up to about 2 lb (0.9 kg), but most are much smaller, only 4.9–5.6 oz (140–160 g). They live to be at least eight years of age.

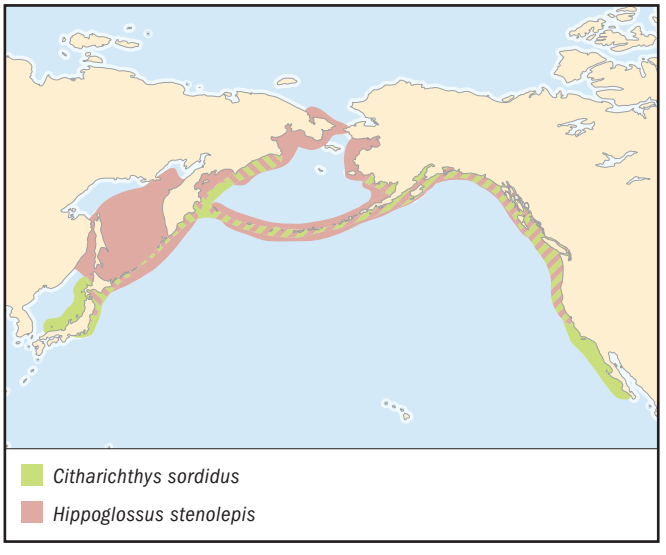
DISTRIBUTION
Marine waters in the northern Pacific Ocean from the Sea of Japan to the Bering Sea and the Aleutian Islands south to Cape San Lucas, Baja California.

HABITAT
Adults inhabit gravel, sand, or mud-sand bottoms at 16.4–1,801 ft (5–549 m) but are most abundant at 164–492 ft (50–150 m); they rarely occur below 984 ft (300 m). Juveniles occur at shallower depths than those occupied by adults and sometimes move into tide pools.

BEHAVIOR
Diurnally active. Spend much of their time on the bottom, although occasionally they are captured at night up in the water column.

FEEDING ECOLOGY AND DIET
Opportunistic, visually oriented predators that feed principally on pelagic crustaceans, such as euphausiids, shrimps, crab larvae, calanoid copepods and amphipods, and occasionally small fishes and benthic prey, among them, annelid worms and crustaceans. Pacific sanddabs are consumed by a variety of larger predators, including blue sharks and other sharks, stingrays, and halibut, and also have appeared in the diets of Guadalupe fur seals.

REPRODUCTIVE BIOLOGY
Begin maturing between ages two and three years. Spawning takes place on or near the bottom from July to September off California. Eggs are released independently, are buoyant, and are fertilized outside the female. Females may spawn more than once during the same spawning season.



CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Excellent food fish. Regarded as a delicacy in California but with less appeal elsewhere. ◆

Summer flounder
Paralichthys dentatus

FAMILY
Paralichthyidae

TAXONOMY
Pleuronectes dentatus Linnaeus, 1766, Carolina, United States.

OTHER COMMON NAMES
English: Fluke; French: Cardeau d'été; Spanish: Falso halibut del Canadá.

PHYSICAL CHARACTERISTICS
Large, sinistral flatfish with a narrow, relatively elongate and thick body. Prominent head with a large terminal mouth with a wide gape and strong canine teeth on both jaws. A rounded or doubly emarginate caudal fin. Eyes are relatively large, separated, and nearly equal in position. Lateral line is arched above the pectoral fin. Scales are small and cycloid, with secondary squamation. Varies in coloration, as individuals change color to match the background of their habitat. Ocular side coloration ranges from drab olive-green to brown to gray; the blind side usually is white. Individuals captured on white sand are nearly completely white, whereas others on dark sediments can be nearly black. Some individuals have pink, green, orange, or brown coloration on the ocular side. The ocular side is marked variously with irregular spots, often with a series of more or less distinct ocelli that are slightly darker than the background coloration, with the most posterior of these arranged in a double triangle (one above and one below the lateral line). Males grow to about 24 in (61 cm) in length, with a weight of 5.7 lb (2.6 kg), and females grow to about 37 in (94 cm) in length, with a weight of 29.5 lb (13.4 kg). Most adults are 15.7–22 in (40–56 cm) in length and weigh between 2.2 and 5.1 lb (1.0–2.3 kg).

DISTRIBUTION
Western North Atlantic in estuarine and continental shelf waters of eastern North America from Nova Scotia to Florida.

HABITAT
Inshore waters, including estuaries and even freshwater (juveniles), bays, harbors, and the inner continental shelf. Summer flounder prefer sandy or muddy bottoms, where they often are found in sand patches near and within eelgrass beds or around pier pilings. Sensitive to low oxygen concentrations and will move out of hypoxic areas (less than 3 ppm oxygen). Concentrated inshore during warmer periods of the year, with smaller fish found in very shallow water. Larger fish in the northern part of the range occur farther offshore, usually at depths of 230–509 ft (70–155 m) and deeper, even during the summer. Estuaries are important nursery areas for this species. Young summer flounder can withstand a wide range of temperatures and salinity levels and are well adapted for estuarine life. Juveniles remain in estuaries until their second year of life in the southern part of their range, but to the north they move just outside them during winter. Many young fish return to the same estuary during their second summer.

BEHAVIOR
Spend most of their lives on or close to the bottom. Occur most often on top of the sediment and do not ever bury deeply. Juveniles may be active at night, but adults appear to be most active during the daytime. Adults undertake strong seasonal inshore-offshore movements, especially in northern regions of the species' geographic range. Adults and juveniles are concentrated in shallow coastal and estuarine waters during the warmer months of the year and remain offshore in deeper waters (to about 492 ft, or 150 m) in the fall and winter, presumably to escape cold winter temperatures. Seasonal movements of summer flounder are complicated and are affected by fish size, location, and stock. Some may spend the winter in deeper bays and channels, and older fish may remain permanently on the outer shelf.

FEEDING ECOLOGY AND DIET
Diurnally active, opportunistic ambush predators. They feed while on the bottom but also rise off the bottom in pursuit of smaller fishes. The primary food of summer flounder is bony fishes, but cephalopods also are important prey of fish larger than 12.2 in (31 cm). Crustaceans, especially mysids and decapods, are important prey for smaller fishes (those fish less than 8.3 in, or 21 cm). Juveniles (3.9–7.9 in, or 10–20 cm) consume mysids, fishes, amphipods, and crabs. Feeding is most active during warmer periods and slows in winter. Spiny dogfish, blue sharks, skates, codfish goosefish, sea robins, bluefish, and winter flounder prey on summer flounder during various stages of their life history.

REPRODUCTIVE BIOLOGY
Male and female summer flounder mature at about 9.8 in (25 cm) and 11 in (28 cm), respectively, corresponding to ages two and a half years for females and two years for males. Many fish may reach maturity at one year. Spawning occurs on or near the bottom, where temperatures range from 53.6 to 66.2°F (12–19°C), and usually takes place during the autumn migration to offshore wintering grounds on the outer continental shelf. Large females (more than 26.8 in, or 68 cm) may produce in excess of four million eggs during a spawning season. Females are serial spawners, continuously producing egg batches that are shed over a period of several months (September to March). Larvae are transported to coastal areas during winter and early spring by prevailing water currents. Post-larvae and young juveniles are found in or near the mouths of estuaries. Metamorphosis is completed within bays and estuaries, where young fish settle to the bottom.

CONSERVATION STATUS
Not threatened. Exploitation of summer flounder by commercial and recreational fishers resulted in stock reductions throughout the species' range during the latter quarter of the past century. Fishery management plans have been developed to conserve and rebuild stocks by limiting commercial and recreational catches through size and season restrictions.

SIGNIFICANCE TO HUMANS
Summer flounder support the most important commercial and recreational fishery for flatfishes along the Atlantic coast of the United States. This highly prized game fish has strong fighting qualities and is excellent table fare. ◆

Pacific halibut
Hippoglossus stenolepis

FAMILY
Pleuronectidae

TAXONOMY
Hippoglossus stenolepis Schmidt, 1904, Aniva Bay, south Sakhalin Island, Sea of Okhotsk.

OTHER COMMON NAMES
English: Northern halibut, right halibut; French: Flétan du Pacifique; Spanish: Fletán del Pacifico.

PHYSICAL CHARACTERISTICS
One of the largest species of flatfishes and among the largest of bony fishes. Typically dextral flatfishes, with a thick, sturdy, elongate, and diamond-shaped body and a highly compressed caudal peduncle with a crescent-shaped caudal fin that often is indented near the edges. The head is large, with a large terminal mouth featuring a wide gape. Nearly symmetrical jaws containing two rows of prominent, conical teeth on the upper jaw and a single row of conical teeth on the lower jaw. The eyes are large, and the upper eye is slightly in advance of the lower one. The lateral line has a high arch above the pectoral fin. Small cycloid scales cover both sides of the body. Ocular side coloration is greenish brown to dark brown or black, marbled with lighter blotches; the blind side usually is white to milky white, sometimes also with blotches. Females reach lengths up to 8 ft, 9 in (267 cm), and weights of about 498 lb (226 kg); males are about 4 ft, 7 in (140 cm) and 220 lb (100 kg). Females grow considerably faster and typically live longer than do males. Almost all halibut larger than 100 lb (45.5 kg) are females. Halibut first become available to the offshore fishery at about five to seven years of age. The oldest recorded age for a male is 55 years, and the oldest recorded age for a female is 42 years.

DISTRIBUTION
Marine waters of the eastern and western North Pacific Ocean. In the west, they are found from the Sea of Japan and Okhotsk Sea north to the Gulf of Anadyr and Chukchi Sea and throughout the Bering Sea. In the eastern Pacific, this species ranges from the Gulf of Alaska southward to about Santa Barbara, California, and, rarely, southward to Point Chamalu, northern Baja California.

HABITAT
Occurs on a variety of bottom types at depths from about 19.7 to 3,609 ft (6–1,100 m) but most commonly found between 180 and 1,385 ft (55–422 m). In summer they are found between 92 and 902 ft (28–275 m) and sometimes shallower, whereas most halibut occur in deeper waters during winter. They have a preferred temperature range of 37.4–46.4°F (3–8°C).

BEHAVIOR
Diurnally active fishes found most often on the bottom. They often rise off the bottom into the water column and may at times even come close to the surface when pursuing prey. Seasonal movements of adults are associated with winter reproduction offshore and summer feeding inshore. Adult halibut move seasonally from deep water to the edge of the continental shelf and then to shallower banks and coastal waters during the summer; they move back to deep water in the winter. Migrations may be extensive—the longest migration on record was that of a fish tagged near Atka Island in the Aleutian Islands, which was recaptured at Coos Bay, Oregon, a distance of 2,500 mi (4023 km).

FEEDING ECOLOGY AND DIET
Large, powerful, opportunistic, visual feeder that consumes a wide variety of prey, including fishes, crabs, clams, squids, and other invertebrates. Small halibut eat a variety of benthic prey items and small fishes, with prey size increasing with fish length. Larger halibut consume almost anything they can catch, with fishes constituting a major portion of their diet. They also feed on squid, octopus, and diverse benthic and nektonic fishes, including cods, pollock, rockfishes, sculpins, other flatfishes, and occasionally smaller halibuts. Halibut are eaten by marine mammals, perhaps some sharks, and other halibuts, but because of their large size, they are rarely found as prey for other fish species.

REPRODUCTIVE BIOLOGY
This species spawns in deep water, 902–1,352 ft (275–412 m), at the edge of the continental shelf during winter (November to March). The Gulf of Alaska is an important spawning area. On average, females mature at 12 years of age (range, eight to 16 years), and males mature by about age eight. The number of eggs produced increases with the size of the female. Large females (those more than 250 lb, or 113.4 kg) can produce as many as two million to four million eggs annually. The eggs are buoyant and fertilized externally. Larvae hatch in about 15 days, depending on water temperature; they remain pelagic for four to five months after spawning. Eggs may be encountered anywhere between 131 and 3,068 ft (40–935 m) but are concentrated between 328 and 656 ft (100–200 m). Newly hatched larvae (0.3–0.6 in, or 8–15 mm) usually are found deeper than 656 ft (200 m). Eye migration begins at a length of about 0.7 in (18 mm). By 1.2 in (30 mm) the young fish resemble adults. With growth, young fish rise in the water and are found predominately at about 328 ft (100 m) by three to five months of age. They are transported great distances and move shoreward with currents, where they settle to the bottom at about six to seven months. After about two years, juveniles begin to move into deeper water. Fishes ages two to four years occur primarily at 361 ft (110 m) or shallower, but some at this size also have been taken at depths of 597 ft (182 m) and occasionally deeper.

CONSERVATION STATUS
Not threatened. Exploitation has resulted in stock reductions of this species throughout its range. Commercial and recreational halibut fisheries are highly regulated, with size and seasonal limitations employed to attempt to keep stocks from diminishing further or disappearing altogether.

SIGNIFICANCE TO HUMANS
Largest and most commercially important flatfish in the North Pacific Ocean. Excellent table fare highly prized by consumers. A commercial fishery for halibut has existed for longer than 100 years. ◆

Plaice
Pleuronectes platessa

FAMILY
Pleuronectidae

TAXONOMY
Pleuronectes platessa Linnaeus, 1758, European seas.

OTHER COMMON NAMES
English: European plaice; French: Plie d'Europe, carrelet; German: Scholle; Spanish: Solla europea.

PHYSICAL CHARACTERISTICS
Dextral flatfish with a deep, oval body; a relatively large head; large eyes; a small mouth; and a series of four to seven bony knobs on the head along a curved line from the eyes back to the lateral line. Teeth are best developed on the jaws of the blind side. Strong, molariform pharyngeal teeth are present on the gill arches. Lateral line is curved slightly above the pectoral fin. Scales are cycloid on both sides of the body. Distinctive ocular side coloration, consisting of a uniformly brown background with brilliant red or orange spots. Blind side usually is

uniformly white. The species can reach lengths to about 39.4 in (100 cm) and weights up to 7.9 lb (3.6 kg), but most adults average only about 13.8–19.7 in (35–50 cm) and weights of about 2.2 lb (1 kg). Individuals can reach at least 30 years of age, but most are much younger. Females grow faster and live longer than males, which rarely live longer than 10–12 years.

DISTRIBUTION
Northeastern Atlantic Ocean in marine and sometimes estuarine waters from the White and Barents Seas southward to the North Sea, including the British Isles and western Baltic Sea; off Iceland; occasionally off Greenland; and along the European coast from Germany and Denmark south to Spain and Portugal and in the western Mediterranean Sea.

HABITAT
Usually found on the inner continental shelf from shallow waters to about 656 ft (200 m) but most abundant in 33–164 ft (10–50 m); usually occur in waters of 35.6–59°F (2–15°C). Most commonly found on sandy sediments but also occur on mud or gravel bottoms. Newly settled plaice recruit to inshore waters typically between 9.8 and 88.6 ft (3–27 m), and sometimes juveniles are found in sandy intertidal pools. Plaice can tolerate reduced salinity levels but do not usually penetrate estuaries to any great degree and are not typically found in freshwater reaches within estuaries. During their first year, young plaice generally are found in shallow waters. By their second year, they begin to move to deeper waters. Older and larger plaice tend to live deeper than smaller and younger plaice.

BEHAVIOR
A diurnally active, benthic fish that lies partially buried when possible. Plaice remain stationary for long periods of time, lying partially buried in the sediment. They are often active at night, especially in shallow water, and have been reported to exhibit homing behavior, at least in near-shore environments. Where there are tidal currents, the plaice orientates itself by pointing into the current and retains its position by pressing its dorsal and anal fins against the bottom. Many individuals congregate in the same general area. Plaice, including larger individuals, sometimes move on rising tides into intertidal areas to forage, retreating with the receding tide.

FEEDING ECOLOGY AND DIET
Opportunistic, visual predators that feed mainly during daylight hours. After metamorphosis, juvenile plaice consume small polychaete worms and harpacticoid copepods, but with increasing size their diet broadens to include a wider variety of prey, such as small crustaceans, amphipods, cumaceans, and small mollusks. Larger plaice consume a greater proportion of thin-shelled bivalve mollusks, especially the siphons of burrowing species (which they nip off using the teeth of their blind-side jaws), as well as gastropod mollusks, shrimps, small crabs, and various polychaete worms. Feeding activity varies with season (temperature), with higher feeding rates occurring during warmer periods than during wintertime. The plaice takes its food in a nearly horizontal position, with its head raised slightly off the bottom. Predators that consume plaice include sculpins, lumpfish, spiny dogfish, weaver fish, seals, and cormorants. Shrimps and ctenophores prey on plaice in the early-life stages.

REPRODUCTIVE BIOLOGY
Maturity schedules vary, depending upon the area where the fish live, their food supply, and ambient temperatures. Female plaice reach sexual maturity between three and seven years of age (11.8–15.7 in, or 30–40 cm) and males at two to six years of age (7.9–11.8 in, or 20–30 cm) in the North Sea. Plaice spawn throughout their range, usually on well-defined spawning grounds. The spawning season varies with latitude and location but usually occurs in the early months of the year throughout its range (December to March in the North Sea, February to March off Denmark, and March to April off Iceland), when water temperatures are about 42.8°F (6°C). Mature fish may undertake extensive migrations from feeding grounds to discrete spawning grounds. The extent of migration depends upon the individual stocks. Spawning grounds generally are located at depths of 66–131 ft (20–40 m). Males and females may pair up and swim one above the other during spawning. Plaice do not guard a nest but rather scatter eggs, which may number up to 50,000 during a spawning event. Eggs are planktonic at first, gradually sinking as development proceeds. Hatching occurs in 18–21 days, depending on temperature. The larval stage lasts between four and six weeks, after which the fish metamorphose at about 0.4–0.7 in (10–17 mm) in length.

CONSERVATION STATUS
Not threatened, although stock sizes have declined over time as a result of overfishing, habitat destruction, and pollution.

SIGNIFICANCE TO HUMANS
One of the most familiar flatfishes in northern European waters, highly desired owing to its size, abundance, and edible qualities. It is the single most important commercial flatfish to the fisheries of Europe. The species also is targeted by a large recreational fishery. Plaice are considered a potential species for aquaculture and are kept as an aquarium species. ◆

Winter flounder
Pseudopleuronectes americanus

FAMILY
Pleuronectidae

TAXONOMY
Pleuronectes americanus Walbaum, 1792, New York.

OTHER COMMON NAMES
English: Blackback, Georges Bank flounder, lemon sole, rough flounder; French: Limande-plie rouge; Spanish: Solla roja.

PHYSICAL CHARACTERISTICS
Medium-sized, dextral flatfish with an oval and thick body with a relatively wide caudal peduncle and a broadly rounded caudal fin. The head is relatively small, with a small terminal mouth with a small gape and thick, fleshy lips. Jaws on the blind side are equipped with a series of incisor-like teeth, whereas the jaws on the ocular side are toothless or nearly so. The lateral line is nearly straight, with only a slight arch above the pectoral fin. Ocular side scales are ctenoid, whereas blind side scales are ctenoid in males and cycloid in juveniles and females. Winter flounder vary in color, depending on the bottom where they live. Larger specimens are dark muddy brown or reddish brown, olive-green, or slate-colored to almost black. On the ocular side, coloration varies from uniformly pigmented to patterned with definite flecks, spots, and darker blotches of differing hues, depending on the bottom type. The blind side usually is uniformly white and translucent with a bluish tinge toward the body margins and sometimes with yellow on the caudal peduncle. Winter flounder can attain a length of 24.8–26.4 in (63–67 cm) and weights to about 7.9 lb (3.6 kg). Winter flounder are relatively long lived, reaching a maximum age of about 15 years. After about age five, females begin to grow faster than males; they also live longer than males.

DISTRIBUTION
Western North Atlantic in estuarine and marine waters along the Atlantic coast of North America from Labrador south to Georgia and also on the offshore banks. Most abundant between the Gulf of Saint Lawrence and Chesapeake Bay.

HABITAT
Brackish waters of tidal rivers, estuaries, and river mouths to areas on the inner continental shelf. Larger and older fish tend to inhabit deeper waters than do younger, smaller fish. Typical inshore habitats consist of muddy sand, especially where the sand is broken by patches of eelgrass; clean sand; clay; and pebbly and gravelly ground. Offshore, winter flounder usually are found on hard bottom. They can survive a wide range of temperatures, from nearly the freezing point of saltwater to about 68–69.8°F (20–21°C). Their blood serum contains an antifreeze protein that helps protect them against freezing.

BEHAVIOR
Diurnally active, with activity beginning at sunrise. At night they lie flat, with heads resting on the bottom and eye turrets retracted. On muddy bottoms, winter flounder usually lie buried, all but the eyes, working themselves down into the mud soon after settling on the bottom. Fish living on tidal flats typically remain motionless during low tides but actively forage during high tides. Can change color to match background surroundings, ranging from whitish on white backgrounds to dark brown or nearly black on dark sediments. Local conditions in inshore waters appear to determine inshore distribution patterns, whereas offshore movements seem to be associated with extreme summer and winter conditions. In general, in summer months adult winter flounder stay in the shallow shore zone when the water temperature is not excessive and food availability is adequate. If these conditions are not met, they may move into deeper channels or offshore or may take evasive action. During winter in the southern parts of their range, they remain or move into shallow water to spawn, whereas in northern regions they remain inshore in protected areas and move offshore in exposed areas to avoid turbulence and drifting pack ice. Winter flounder in deeper waters, such as Georges Bank, remain there year-round. Winter flounder bury in sediments when water temperatures are below 32°F (0°C) and ice crystals are present in the water. They are active at water temperatures up to 71.6°F (22°C), beyond which they become inactive. They are sensitive to low levels (3 ppm) of dissolved oxygen.

FEEDING ECOLOGY AND DIET
Visual predators. Consume a wide variety of small invertebrates and, rarely, small fishes, such as sand lance. Principal food includes polychaetes, anthozoans, and amphipods but also shrimps, small crabs and other crustaceans, ascidians, holothurians, squids, bivalve and gastropod mollusks, and sometimes fish eggs. They often bite off clam siphons that protrude from the sand. While feeding, a winter flounder lies with its head raised off the bottom with its anterior body braced vertically against the bottom. Eye turrets are extended, and the eyes move independently of each other. After sighting its prey, the fish remains stationary, pointed toward the target, and then lunges forward and downward to seize its prey. Winter flounder are eaten by codfish, spiny dogfish, goosefish, hakes, winter skate, smooth dogfish, striped bass, bluefish, sea raven, seals, ospreys, gulls, blue herons, and cormorants.

REPRODUCTIVE BIOLOGY
In the fall, as gonads ripen, adult winter flounder remain in or move into shallow water to spawn. They spawn in winter in southern locations and in early spring (January to May) in more northern locations. Spawning in inshore waters occurs nearly at the seasonal lowest temperatures, which range from 31.1 to 35.6°F (−0.5–2.0°C), depending on latitude. Spawning on Georges Bank happens at temperatures ranging from about 37.9 to 41.9°F (3.3–5.5°C). Winter flounder spawn on sandy bottom and algal mats, often in shallow water. Spawning in estuaries occurs in areas with salinity levels as low as 11.4 ppt. Males mature at age two and females at age three off New York, when fish are 7.9–9.8 in (20–25 cm) in total length. Fish in more northern areas mature later—age three years and four months for males and three years and six months for females north of Cape Cod and age six for males and seven for females in Newfoundland. Maturity seems to be a function of size rather than age. On Georges Bank, the mean age at maturity is just under two years for both sexes.

Females produce, on average, 500,000 eggs, but larger fish can produce up to 3.5 million eggs. Winter flounder migrate into shallow water or estuaries and coastal ponds to spawn, and tagging studies show that most return repeatedly to the same spawning grounds. They are batch spawners. Females in captivity spawned up to 40 times and males up to 147 times. Males initiated all observed spawning events, which occurred throughout the night but primarily between sunset and midnight. Spawning by one pair frequently elicited sudden convergence and spawning by secondary males. Strict pair spawning is uncommon. Male and female activity patterns were almost entirely nocturnal during the reproductive season but became increasingly diurnal during the post-spawning season. Eggs are fertilized outside the body and sink to the bottom, where they stick together in clusters. Incubation takes place over 15–18 days at 37–37.9°F (2.8–3.3°C). Young larvae hatch at about 0.12–0.14 in (3.0–3.5 mm). Metamorphosis is complete when larvae are only 0.31–0.35 in (8–9 mm) long. Winter flounder exhibit little movement from areas where they settle, unless seasonal temperatures become extreme.

CONSERVATION STATUS
Not threatened, although their numbers have diminished substantially since the 1970s, and the stocks throughout most, if

not all, of the species' range are considered to be overexploited. Overfishing, pollution, and habitat destruction all contribute to reductions in stock sizes of this species. Current fishery management plans are to restore stock sizes to former levels. As of 2002 little success was evident in these attempts.

SIGNIFICANCE TO HUMANS
Highly desirable commercial and recreational species. Winter flounder were the most frequently captured flatfish taken by recreational fishers along the eastern coast of the United States until about 1970. Since then, landings of fish in both commercial and recreational fisheries have declined substantially. ◆

Windowpane flounder
Scophthalmus aquosus

FAMILY
Scophthalmidae

TAXONOMY
Pleuronectes aquosus Mitchill, 1815, New York, United States.

OTHER COMMON NAMES
English: Sand dab; spotted flounder, brill; French: Turbot de sable.

PHYSICAL CHARACTERISTICS
Medium-sized, sinistral flatfish characterized by a deep, nearly round, thin, and almost translucent body with a rounded caudal fin. The head is small with a relatively large mouth having a wide gape and with a projecting lower jaw that has a knob on its ventral surface. Small teeth are present on both jaws. The first 10–12 fin rays of the dorsal fin are free from the fin membrane along the distal half and branched toward their tips, forming a conspicuous fringe. Eyes are large, separated, and nearly equal in position on the head. Pelvic fin bases are elongated and slightly asymmetrical. Scales are cycloid and smooth to the touch. The lateral line is strongly arched above the pectoral fin. The ocular side is rather translucent greenish olive or slightly reddish brown or pale slate-brown, mottled with darker and paler irregular markings and usually dotted with many small, irregularly shaped brown spots and sometimes also with white spots that vary in size. Blind side is generally whitish, occasionally with some irregular darker blotches. Can reach sizes to about 15.7 in (40 cm) and weights to about 2.2 lb (1 kg), but adults typically average only 9.8–11.8 in (25–30 cm). Can live to be 15–18 years of age, but most individuals are 11 years old or younger.

DISTRIBUTION
Western North Atlantic in lower estuarine and marine waters on the inner continental shelf of eastern North America from the Gulf of Saint Lawrence to Florida. Most abundant from Georges Bank to Chesapeake Bay.

HABITAT
Shallow, inshore waters from the high tide line down to about 656 ft (200 m), with the greatest numbers occurring at depths of less than 180 ft (55 m). They occur most often on sandy bottoms but also can be found on softer and muddier sediments.

BEHAVIOR
Diurnally active. Often lie on or within sandy sediments. Young windowpane flounder settle in shallow water inshore and tend to move into deeper offshore waters as they grow. Adults may undertake movements along the coast for considerable distances (80 mi, or 129 km, in three months) or even move across open water.

FEEDING ECOLOGY AND DIET
Visually oriented, ambush predators that forage on a variety of actively swimming prey, particularly mysids, various fishes, and decapod crustaceans, especially shrimp. They also eat chaetognaths, squids, mollusks, ascidians, polychaetes isopods, amphipods, euphausiids, and salps. Windowpane flounders, in turn, are eaten by various sharks, skates, stingrays, codfish, cobia, bluefish, and other windowpane flounders.

REPRODUCTIVE BIOLOGY
Windowpane flounder of both sexes mature at about the same size, 8.3–8.7 in (21–22 cm) between ages three and four years, with males sometimes maturing at age two. Spawning occurs from February to November, with peak spawning from May through October. There is a strong correlation between water temperatures and spawning. They spawn in the evening or at night on or near the bottom at temperatures from 42.8 to 69.8°F (6–21°C), with optimal spawning temperatures of 60.8–66.2°F (16–19°C) in the Mid-Atlantic Bight and 55.4–60.8°F (13–16°C) on Georges Bank. Eggs are transparent, have an oil globule, and are buoyant. Larvae hatch at 0.07–0.09 in (1.8–2.3 mm), usually at eight days post-spawning in temperatures of 50–55.4°F (10–13°C). Eye migration begins when they reach a length of about 0.26 in (6.5 mm), proceeds very rapidly, and typically is completed by 0.39–0.51 (10–13 mm) total length.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Not commercially important and not targeted directly by commercial fisheries. They often are taken as by-catch during trawl fishing. ◆

Common sole
Solea solea

FAMILY
Soleidae

TAXONOMY
Pleuronectes solea Linnaeus, 1758, European ocean.

OTHER COMMON NAMES
English: Dover sole; French: Sole commune; German: Seezunge; Spanish: Lenguado commúne.

PHYSICAL CHARACTERISTICS
Dextral flatfish with an elongate but rather thick body. The dorsal fin extends to the anterior part of the head, often to a point equal to a horizontal line drawn through the upper eye. Has a smoothly rounded head, projecting snout, and a small, subterminal mouth with small teeth and with the preoperculum covered by skin. On the blind side, head and snout are covered with close-set, whitish sensory papillae. Moderately large pectoral fins. On the ocular side this fin has a distinct elliptical black patch (not surrounded by white ring) on its upper extremity. On the blind side it is only slightly smaller than the ocular side counterpart. Last rays of the dorsal and anal

fins are joined to the base of the caudal fin by a distinct membrane, and the last rays of the dorsal and anal fins overlap the bases of the caudal fin rays. Ocular side is uniformly dark brown or grayish brown, with numerous darker irregular blotches. Dorsal and anal fins are edged in white. Blind side is creamy white. Lengths reach about 27.6 in (70 cm) and weights about 6.6 lb (3 kg), but most fish are 11.8–15.7 in (30–40 cm) in length. They attain ages up to seven to eight years and perhaps older.

DISTRIBUTION

Northeastern Atlantic in estuarine and marine waters from off Norway and the western Baltic Sea and commonly off Ireland, England, and Scotland (uncommon northwest of Scotland). Also commonly along the European coast in the southern North Sea, the Mediterranean Sea, and the eastern Black Sea and southward to Senegal.

HABITAT

Occurs on soft sandy or muddy bottoms over a wide range of salinity levels and depths, ranging from shallow estuarine waters of 3.3 ft (1 m) or less down to about 656 ft (200 m). Estuaries are important nursery areas for newly settled fish and juveniles. Young-of-the-year soles appear in surf zone waters on shallow sandy beaches during summertime and can be taken even in shallow tide pools during this time. They occur at temperatures from 46.4 to 75.2°F (8–24°C). Adults and larger juveniles undertake seasonal migrations between shallower waters on the inner shelf (in warmer periods) to deeper areas (230–427 ft, or 70–130 m) on the outer shelf in winter. Larger fish generally are found in deeper waters than are smaller fish. Seasonal inshore migrations during springtime are complicated, because larger fish, besides moving inshore, also move toward definite spawning grounds. Young fish move into inshore waters earlier, usually during spring, whereas larger fishes move into shallower waters by late spring or early summer.

BEHAVIOR

Benthic fishes that live somewhat solitary lives. They spend much of the daylight hours partially buried in sediments or lying on top of them. In overcast conditions or in turbid waters, such as in estuaries, they are more active during daylight hours. Generally, they are most active at nighttime, when they sometimes are found off the bottom and up in the water column. They are found pelagically during migrations.

FEEDING ECOLOGY AND DIET

Opportunistic, nocturnal feeders that rely on chemosensory and tactile information to locate their prey. Some feeding by adults and juveniles also takes place during daylight hours when fish are active. In some estuaries, feeding activity showed a strong relationship to the tidal cycle. Juveniles may use intertidal areas as feeding grounds during flood tides. They consume a diverse array of mostly benthic prey, including amphipods, polychaetes, oligochaetes, small bivalve mollusks and siphons of bivalve mollusks, gastropod mollusks, mysids and crangonid shrimps, brittle starfish, and, to a lesser extent, small benthic fishes, such as sand eels (*Ammodytes*) and gobies. Diets often vary between habitats and in terms of size of fish, with prey sizes generally increasing with increasing fish size. Soles feed on small quantities of prey very often. Predators of sole include spiny dogfish, hakes, lizardfish, codfish, weaver fish, and cormorants.

REPRODUCTIVE BIOLOGY

Mature at three to five years of age and at sizes of about 9.1–11.8 in (23–30 cm). Spawn primarily during one well-defined season in the spring and early summer, which varies according to latitude (March to May off England and April to June farther north). Spawning grounds are located in both shallow and deep waters. Spawning takes place between 42.8 and 53.6°F (6–12°C). Females may release up to 100,000 eggs during a spawning event. Eggs are buoyant and pelagic; planktonic larvae hatch when eggs reach a length of about 0.12–0.16 in (3–4 mm). Metamorphosis occurs at about 0.47–0.59 in (12–15 mm), with settlement taking place at 0.59–0.7 in (15–18 mm) in length. Adults undertake migrations to definite spawning grounds located on the inner continental shelf at depths of 131–197 ft (40–60 m). Spawning grounds have been identified in the North Sea, the Irish Sea, and the English Channel.

CONSERVATION STATUS

Not threatened. Stock sizes have been reduced owing to overfishing. At present, efforts have focused on limiting fishing pressure and reducing mortalities, with expectations that stock sizes will not decline further.

SIGNIFICANCE TO HUMANS

Abundant and valued food species. The most valuable fishing grounds lie in the southern and central North Sea and the Bay of Biscay. Little recreational fishing occurs, primarily because of this species' nocturnal feeding habits and also because of the difficulty in catching it. ◆

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Tetraodontiformes

(Pufferfishes, triggerfishes, and relatives)

Class Actinopterygii
Order Tetraodontiformes
Number of families 9

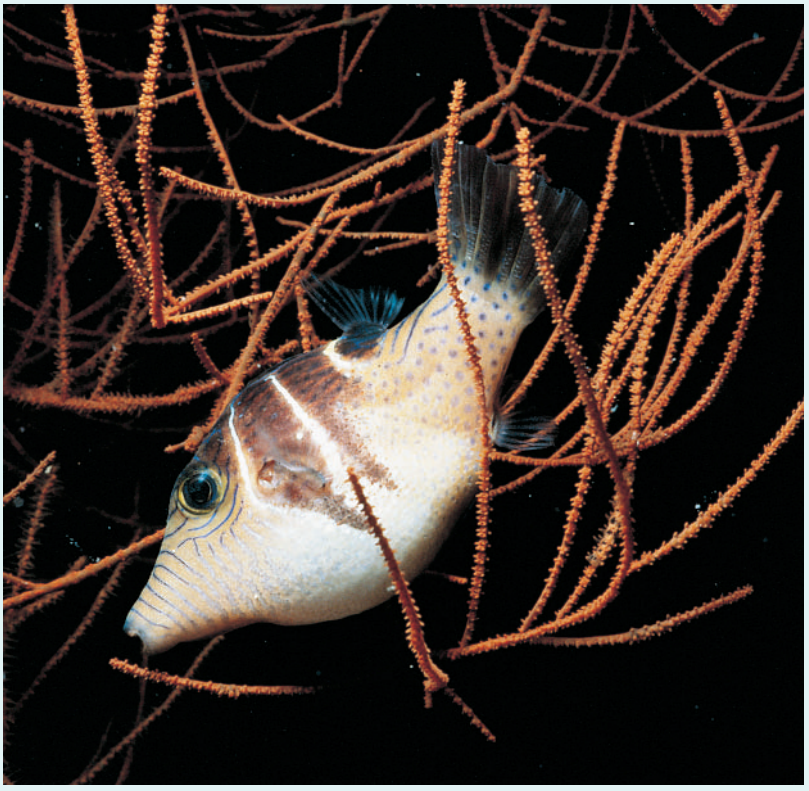


Photo: A whitespotted filefish (*Cantherhines macrocerus*) sleeping, with dead fire coral in its mouth, at night, near the Los Rocas Islands of Venezuela. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Although it is remarkably derived, this order of fishes dates from the early Eocene epoch or, possibly, the late Cretaceous period. There are nine families, including the spikefishes (Triacanthodidae, 11 genera and 21 species), the triplespines (Triacanthidae, four genera and seven spp.), the boxfishes (Ostraciidae, 11 genera and 37 spp.), the filefishes and leatherjackets (Monacanthidae, 25 genera and at least 104 spp.), the triggerfishes (Balistidae, 12 genera and at least 37 spp.), the threetooth puffer (Triodontidae, one genus and one species), the pufferfishes (Tetraodontidae, 26 genera and at least 170 species, with one species that has two subspecies), the porcupinefishes (Diodontidae, seven genera and 20 spp.), and the molas or ocean sunfishes (Molidae, three genera and four spp.).

Physical characteristics

There is some variability within this order, but all are distinguished by fused teeth within their jaws. Spikefishes are compressed, high bodied (great in depth), or elongate; some have concave foreheads and others elongated, tubelike snouts. The caudal fin is rounded to truncated, and there are 12–18 soft rays in the dorsal fin and 11–16 rays in the anal fin. Coloring is orange, yellow, or pink. Triplespines are compressed and elongate, with steeply sloping foreheads, narrow caudal peduncles, and forked tails. The first dorsal spine is large. The coloring is silvery, with hints of yellow or pale olive. The boxfishes are indeed boxlike, with bodies covered in bony-like plates. They have large rounded or truncated caudal fins and the ability, in numerous species, to secrete ostracitoxin (a poison that makes the creature unpalatable) as an anti-predatation mechanism. Some species have horns that protrude from their heads. A few species are brightly colored, but most are dull or cryptic.

Filefishes and leatherjackets also vary in shape and appearance. Generally, they are compressed and somewhat elongate, and they may have steeply sloped foreheads. Others are rhomboid in shape. At least one species, *Anacanthus barbatus*, is long and slender and resembles superficially a pipefish (Sygnathidae). The first dorsal spine usually is tall and strong. The caudal fin is truncated or slightly rounded. Color patterns vary, ranging from bright colors to cryptic or nondescript shades. Triggerfishes are compressed, rhomboid, or slightly elongate, with pelvic fins that are fused into a single spine. The first dorsal spine is capable of locking by using the second spine as a trigger that locks it into place. It is used as an anti-predation mechanism. The eyes can rotate independently of each other. Color patterns also vary and may be spectacular and bright or quite dull or cryptic.

The threetooth puffer has a beak consisting of three fused teeth, with a median suture in the upper jaw. The body is

A shy toby (*Canthigaster ocellicincta*) sleeps in the Gorgonian coral at night in the South China Sea near the Sipadan Island of Borneo. (Photo by Jeff Rotman/Photo Researchers, Inc. Reproduced by permission.)

elongate, compressed, and inflatable. The caudal penduncle is long, and the caudal fin forked. Pufferfishes have four teeth fused together to form a beak, but there are medial sutures in both the upper and lower jaws. Their bodies are elongate, usually compressed or rhomboid in shape, and inflatable. There are seven to 18 soft rays in both the dorsal and anal fins, respectively. Many species have small prickles on the skin of their bellies. Their skin, entrails, and sometimes their flesh may contain tetraodotoxin, an anti-predation poison that is highly toxic. Porcupinefishes are large, elongate, robust, and somewhat boxlike, and they are capable of inflation. They have numerous spines along the body. The two teeth on their jaws are fused into a beak. Molas are large, compressed, and typically high-bodied fishes, with jaws that support two fused teeth. The caudal fin may be replaced by a clavus, which is used to stablize the fish when swimming. The dorsal and anal fins are set high. Both the lateral line and swimbladder are missing from adults.

Distribution

Members of this order occur in marine, brackish, and freshwater of the tropics, subtropics, and temperate zones. The spikefishes are tropical and subtropical deepwater residents of the western Atlantic and Indo-Pacific regions. Triplespines occur in shallow marine and brackish waters of the Indo-Pacific region. Boxfishes, triggerfishes, filefishes, and leatherjackets are distributed widely, mainly in coastal waters of the tropical, subtropical, and temperate or warm temperate Atlantic, Indian, and Pacific Oceans. The monotypic threetooth puffer is a deep-slope species of the Indo-Pacific region. Marine pufferfishes occur in tropical and subtropical waters of the Atlantic, Indian, and Pacific Oceans; numerous species enter brackish water or even freshwater. Some strictly freshwater species are found in river systems of Africa, Asia, or South America. Porcupinefishes occur in tropical, subtropical, and warm temperate waters of the Atlantic and Indo-Pacific regions; at least one species is circumglobal in its distribution. Molas also are found in tropical, subtropical, and warm temperate waters of the Atlantic, Indian, and Pacific Oceans but are largely pelagic and venture inshore only occasionally.

Habitat

A birdbeak burrfish (*Cyclichthys orbicularis*) in the waters of Indonesia. (Photo by Michael Aw/The Photo Library-Sydney/Photo Researchers, Inc. Reproduced by permission.)

Habitat preferences and utilization vary widely within this order. Most species are marine, but at least 20 occur in freshwater systems. Spikefishes are bottom dwelling in relatively deep waters. Triplespines also live on the bottom but on shallow marine and brackish water sand flats and mudflats. Boxfishes frequent coral or rocky reefs in relatively shallow water; others occur on sea grass flats and algae beds. Large postlarvae or young juveniles of some species are pelagic and are part of the diet of tunas and billfishes; others enter estuaries. Triggerfishes also are associated with coral or rocky reefs but may be found on rubble and sand flats. Some species are pelagic or semipelagic, the latter dwelling in the water column but seeking shelter in holes on the bottom or along walls. Filefishes and leatherjackets are quite wide ranging in their habitat use. Many species are associated with coral or rocky reefs; others with sponge reefs, sea grass flats, algae beds, or rubble and sand flats; and still others dwell in the water column. The threetooth puffer is a benthic, deep-slope-dwelling fish. Marine and brackish water pufferfishes occur on coral and rocky reefs, on rubble, sand, mud, or sea grass flats; on algae beds; or in the water column. Freshwater species tend to be benthic. Porcupinefishes occur on coral and rocky reefs, usually to seaward, and also utilize caves and holes in relatively shallow water. They also frequent reefs dominated by sponges. The molas are pelagic fishes that prefer the upper depths of the open ocean but also venture inshore, especially near deep-slope habitats that experience upwelling of deeper, cooler water.

Behavior

To some extent, tetraodontiform fishes incorporate their unique body structure and abilities into their patterns of behavior. For defense, feeding, social interaction, or reproduction, they rely variously on body armament; their fused beaks or ability to inflate with water; or their color patterns, which may advertise toxicity. Adult boxfishes utilize their body armor and ability to secrete ostracitoxin, a compound poisonous to predators (and other fishes, including themselves, if they are kept in a confined space), as defensive mechanisms. Thus, predation risk is minimized as they swim along the bottom or up into the water column. Despite reduction in risk, however, numerous species are quite cryptic as they move about in algae or corals. Boxfishes also are territorial. A majority of triggerfishes are colorful, solitary, and quite aggressive in the defense of their territories. Those species that dwell in the water column often assemble in loose aggregations of up to hundreds of individuals as they forage off walls or along deep slopes. These species quickly retreat to individual shelters when threatened, however.

A honeycomb cowfish (*Lactophrys polygonius*) by coral near Bonaire. (Photo by Charles V. Angelo/Photo Researchers, Inc. Reproduced by permission.)

An inflated spotted puffer, or guinea fowl puffer (*Arothron meleagris*), swimming near Hawaii. (Photo byAndrew G. Wood/Photo Researchers, Inc. Reproduced by permission.)

Filefishes and leatherjackets are solitary or gather in small groups, but some form monogamous pairs that patrol a home range or territory. Others, such as *Aluterus monoceros*, form large schools. Many species are cryptic as well and take advantage of structure to mask their movements. A few species, such as juvenile *Aluterus scriptus*, swim on their sides and mimic floating leaves or other vegetation. Some swim openly in the water column, however. The color pattern of some filefishes and leatherjackets may be put to a surprising advantage. For example, the mimic filefish, *Paraluteres prionurus*, mimics the toxic saddled puffer, *Canthigaster valentini*, and thus avoids predation. Another species, the diamond filefish (*Rudarius excelsius*) mimics benthic algae.

Pufferfishes are solitary or paired or form small groups or schools. Many species utilize color pattern to advertise their toxic nature and thus avoid predation. Others are remarkably cryptic and even bury themselves in the sand. Some frequent the water column but return to the bottom for shelter or to feed. All are capable of inflating as a defensive mechanism. When they are not sheltering in holes or caves,

porcupinefishes swim openly in the water column and depend on both their large spines and ability to inflate themselves to defend against predation. They reportedly have toxic flesh or organs that may contribute toward their defense as well. Some species have been observed to bury themselves in the sand. Although they are seen swimming during daylight hours, numerous species also are nocturnal. Molas swim about sideways or upright at or near the surface in the open ocean and, despite their ungainly appearance, are relatively strong and fast swimmers when necessary. They also drift on their sides in the current. When they are inshore near kelp beds, they allow themselves to be cleaned by resident cleanerfish species. The behavior of deep-dwelling spikefishes and threetooth puffers is largely unknown. Presumably, these fishes are largely solitary and move about the bottom or in the water column. The threetooth puffer is able to defend itself by inflation.

Feeding ecology and diet

Feeding patterns and dietary preferences of tetraodontiform fishes also vary. Little is known about spikefish feeding. Those species with long, slender, and highly specialized snouts likely pluck microinvertebrates from the bottom or possibly the water column. Species with relatively larger mouths probably feed on benthic invertebrates. At least one species, *Macrorhamphosodes uradoi*, feeds on the scales of other fishes. Triplespines also eat benthic invertebrates unearthed from sand or mud. Boxfishes are mainly omnivorous and feed upon small invertebrates, especially sessile species, as well as benthic algae. Triggerfishes are more wide ranging in their diet and feed upon benthic invertebrates that include gastropods, bivalves, crustaceans, and various echinoderms. Some species also eat algae, and those that dwell in the water column eat zooplankton. Similarly, filefishes and leatherjackets favor various benthic invertebrates, but some species are specialized to feed upon live corals or zooplankton. The threetooth puffer probably limits its diet to benthic invertebrates. Pufferfishes are remarkable opportunists and feed upon various invertebrates as well as algae. Larger species are quite capable of breaking open hard-shelled organisms, such as gastropods, bivalves, and crustaceans. Some species are specialized for certain invertebrates, however. Porcupinefishes prefer hard-shelled invertebrates, which they crush with their beaks. The molas utilize their parrot-like beaks to feed upon zooplankton and jellyfishes in the water column but also take fishes, mollusks, crustaceans, and brittlestars when they are inshore or near the bottom in deep-slope areas.

Two false-eye puffers (*Canthigaster papua*) courting, preparing a nest in algae on the coral reef, near Papua New Guinea. (Photo by Fred McConnaughey/Photo Researchers, Inc. Reproduced by permission.)

A smooth trunkfish (*Lactophrys triqueter*) eating sargeant major eggs, near St. Vincent, in the Caribbean. (Photo by Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

Most members of this order are preyed upon while in the larva or post-larva stage. As adults, relatively few have predators. Successful predators would have to be tolerant of spines, bony plates, and ossicles formed from fused bones, and, in some families, toxins. Some toxic puffers (Tetraodontidae), however, are preyed upon by sea snakes.

Reproductive biology

Depending upon the species, tetraodontiform fishes have diverse mating systems and spawn demersal or pelagic eggs. Seasonality may be pronounced at higher latitudes or in colder, deeper waters. Reproduction also may be linked to

lunar or semilunar cycles. Little is known of the reproductive biology of the deep-dwelling spikefishes, threetooth puffers, and shallow-dwelling triplespines, but their eggs are likely demersal and their larvae pelagic. Boxfishes have mainly male-dominated mating groups, court and spawn at dusk, and produce pelagic eggs and larvae. Triggerfishes have varying mating systems, including monogamy, bigamy, and polygyny. They usually spawn demersal eggs in nests that are guarded quite aggressively by females or, to a lesser extent, by males. Larvae are pelagic. The filefishes and leatherjackets studied thus far have mating systems that include monogamy, facultative monogamy, polygyny, female visiting within male territories, or promiscuity. They all appear to lay demersal eggs in nests or on algae. There may be male parental care, female parental care, biparental care. or no care of eggs. The larvae are pelagic and may be adapted for an extended pelagic existence.

Pufferfishes have diverse mating systems and patterns of courtship and spawning. The eggs generally are demersal and are laid in nests on algae or scattered on the bottom. The eggs of some species are poisonous. Porcupinefish reproductive behavior appears to vary within as well as between species. Both pair and group (single female and multiple males) spawning has been reported for *Diodon holacanthus*. Courtship begins at dusk, and spawning is pelagic in shallow water and may involve splashing at the surface as eggs and milt are released. Alternately, the eggs may sink to the bottom. The larvae are pelagic as well. Eggs of the genus *Chilomycterus* reportedly are demersal, although their larvae are pelagic. Details of courtship and spawning of molas are not well known. They are highly fecund and produce hundreds of millions of pelagic eggs. The larvae are also pelagic.

Conservation status

A few species are cited on the IUCN Red List. The queen triggerfish, *Balistes vetula* (Balistidae), the Rapa Island toby, *Canthigaster rapaensis* (Tetraodontidae), and the blunthead puffer, *Liosaccus* (= *Sphoeroides*) *pachygaster* (Tetraodontidae), are listed as Vulnerable. Five additional species in the family Tetradontidae are listed as Data Deficient. Various species may be at risk from overfishing (as a target species or as bycatch) or habitat destruction. The European Community prohibits the trade of pufferfish products.

Significance to humans

Numerous species of triggerfishes, filefishes and leatherjackets, pufferfishes, and molas are taken in subsistence and artisinal fisheries. Commercial fisheries exist for certain triplespines, triggerfishes, filefishes and leatherjackets, and pufferfishes. The latter group includes the famous fugu (*Takifugu* spp.), which is esteemed as a delicacy in Japan but poses a serious health risk from tetraodotoxin poisoning if it is not prepared properly. Boxfishes and molas also are or may be poisonous. Various species are used in Chinese medicine. Many species of boxfishes, porcupinefishes, and puffers are taken for use as decorations in the ornamental trade; for example, diodontids are often used to make lamp shades. Some triggerfishes and filefishes and leatherjackets are considered game fishes. Many species of triggerfishes, filefishes and leatherjackets, and pufferfishes (both marine and freshwater) are collected for the aquarium trade, and some are highly valued.

1. Spotted toby (*Canthigaster solandri*); 2. White-spotted puffer (*Arothron hispidus*); 3. Spot-fin porcupinefish (*Diodon hystrix*); 4. Threetooth puffer (*Triodon macropterus*); 5. Mola (*Mola mola*); 6. Yellow boxfish (*Ostracion cubicus*); 7. Fugu (*Takifugu rubripes*); 8. Scrawled filefish (*Aluterus scriptus*). (Illustration by Brian Cressman and Patricia Ferrer)

1. Spikefish (*Halimochirugus alcocki*); 2. Blackbar triggerfish (*Rhinecanthus aculeatus*); 3. Clown triggerfish (*Balistoides conspicillum*); 4. Orange-striped triggerfish (*Balistapus undulatus*); 5. Triplespine (*Triacanthus biaculeatus*); 6. Longnose filefish (*Oxymonacanthus longirostris*); 7. Long-horn cowfish (*Lactoria cornuta*). (Illustration by Bruce Worden)

Species accounts

Orange-striped triggerfish
Balistapus undulatus

FAMILY
Balistidae

TAXONOMY
Balistapus undulatus Park, 1797, Sumatra, Indonesia.

OTHER COMMON NAMES
English: Orange-lined triggerfish; French: Baliste strié; German: Orangestreifen-Drückerfisch; Afrikaans: Oranje streepsnellervis; Japanese: Kumadori.

PHYSICAL CHARACTERISTICS
Body compressed and oblong, the forehead sloping to above the eye, the caudal peduncle compressed, with a truncate caudal fin. There are three spines, 24–27 soft rays in the dorsal fin, and 20–24 soft rays in the anal fin. The first dorsal spine can be locked. Body color variably green to dark green or dark brown. There is a pattern of orange lines that curve obliquely on the posterior portion of the head and along the body. A band of orange and blue stripes runs obliquely from the mouth to below the pectoral fin. There is a large black blotch on the caudal peduncle. The caudal fin and soft fin rays of the dorsal, anal, and pectoral fins are orange. Grows to at least 11.8 in (30 cm) in total length.

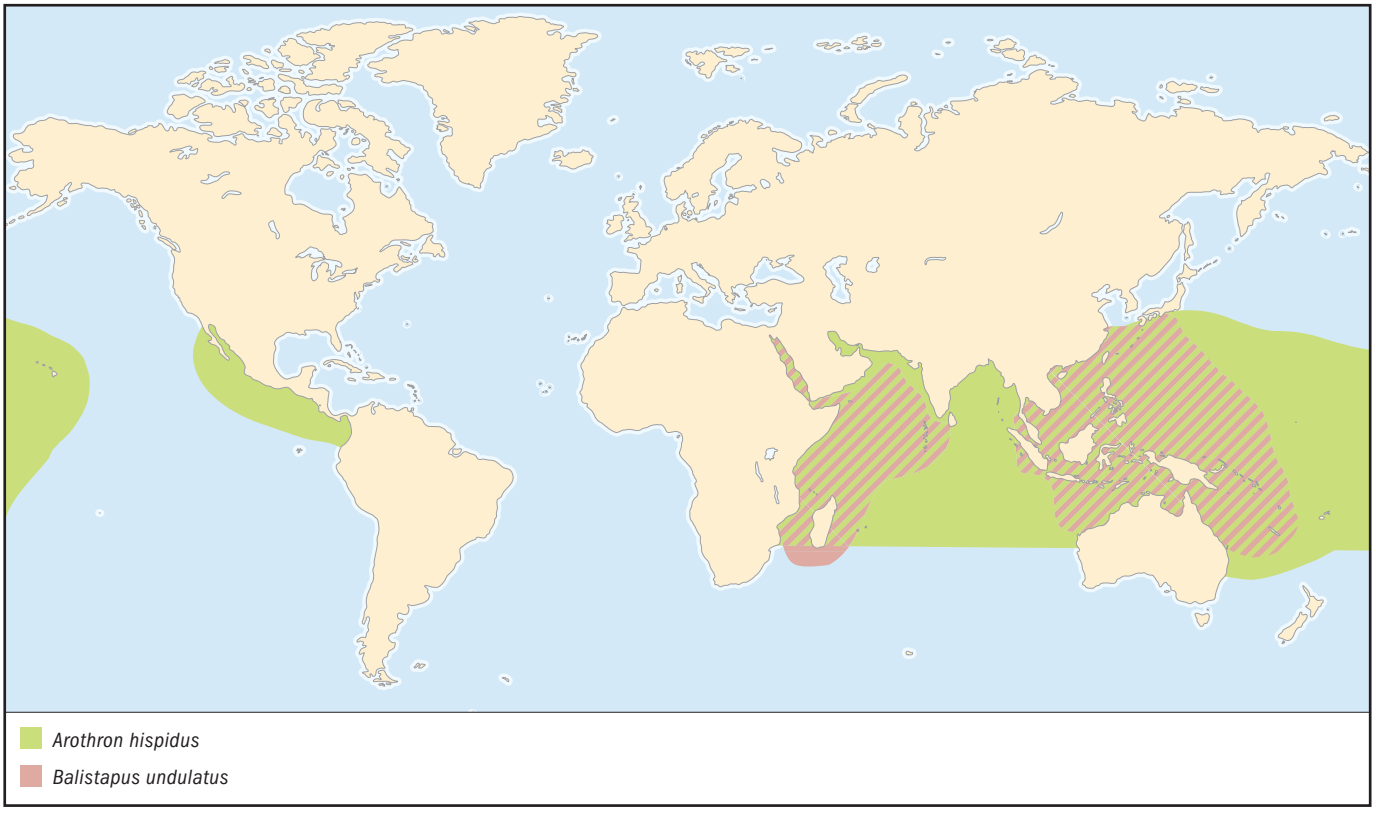
DISTRIBUTION
Tropical and subtropical Indo-West Pacific from the Red Sea and East Africa south to Natal in South Africa, east through Micronesia and the Line Islands to the Marquesas and the Tuamotu Archipelago in eastern Polynesia, south to the Great Barrier Reef of Australia and New Caledonia, and north to southern Japan. New research suggests that populations in the western Indian Ocean, the Indo-Malayan region, and the Pacific may constitute three distinct species.

HABITAT
Somewhat ubiquitous on reefs; may be found on seaward or protected reefs and in lagoons at depths ranging from about 6.6 to 164 ft (2–50 m).

BEHAVIOR
Territorial and generally solitary, although individuals may live in somewhat close proximity to one another and have overlapping home ranges.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on sponges, hydrozoans, tunicates, mollusks, echinoderms, small fishes, and algae.

REPRODUCTIVE BIOLOGY
Pair-spawns, with a single cluster of eggs deposited in a shallow nest excavated in rubble or sand. Larvae are pelagic.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A minor commercial or subsistence food fish in some areas that is either dried and salted or sold fresh. Also collected for the aquarium trade. ◆

Clown triggerfish
Balistoides conspicillum

FAMILY
Balistidae

TAXONOMY
Balistoides conspicillum Bloch and Schneider, 1801, Indian and American seas.

OTHER COMMON NAMES
French: Baliste lépreaux; German: Leoparden-Drückerfisch; Afrikaans: Nas-snellervis; Japanese: Mongarakawahagi.

PHYSICAL CHARACTERISTICS
Body and caudal peduncle are compressed; the body is robust and oval in shape. There are three spines and 25–27 soft rays in the dorsal fin as well as the anal fin. The first dorsal spine can be locked into an erect position. The caudal fin is somewhat rhomboid in shape. The body's color pattern is unmistakable. The background color is black, with large white spots along the flank, a white breast and band below the eye, a white caudal peduncle, and an alternating pattern of black, white, and black on the caudal fin. The mouth is yellow or orangish yellow, with a thin yellow stripe on a black background. Faint yellow hues are found along the base of the anal fin and on the caudal peduncle. The dorsal, lower anal, pectoral, and pelvic fins are white. Grows to at least 19.7 in (50 cm) in total length.

DISTRIBUTION
Tropical and subtropical Indo-West Pacific from East Africa and South Africa east to Samoa, south to northern Australia and New Caledonia, and north to southern Japan.

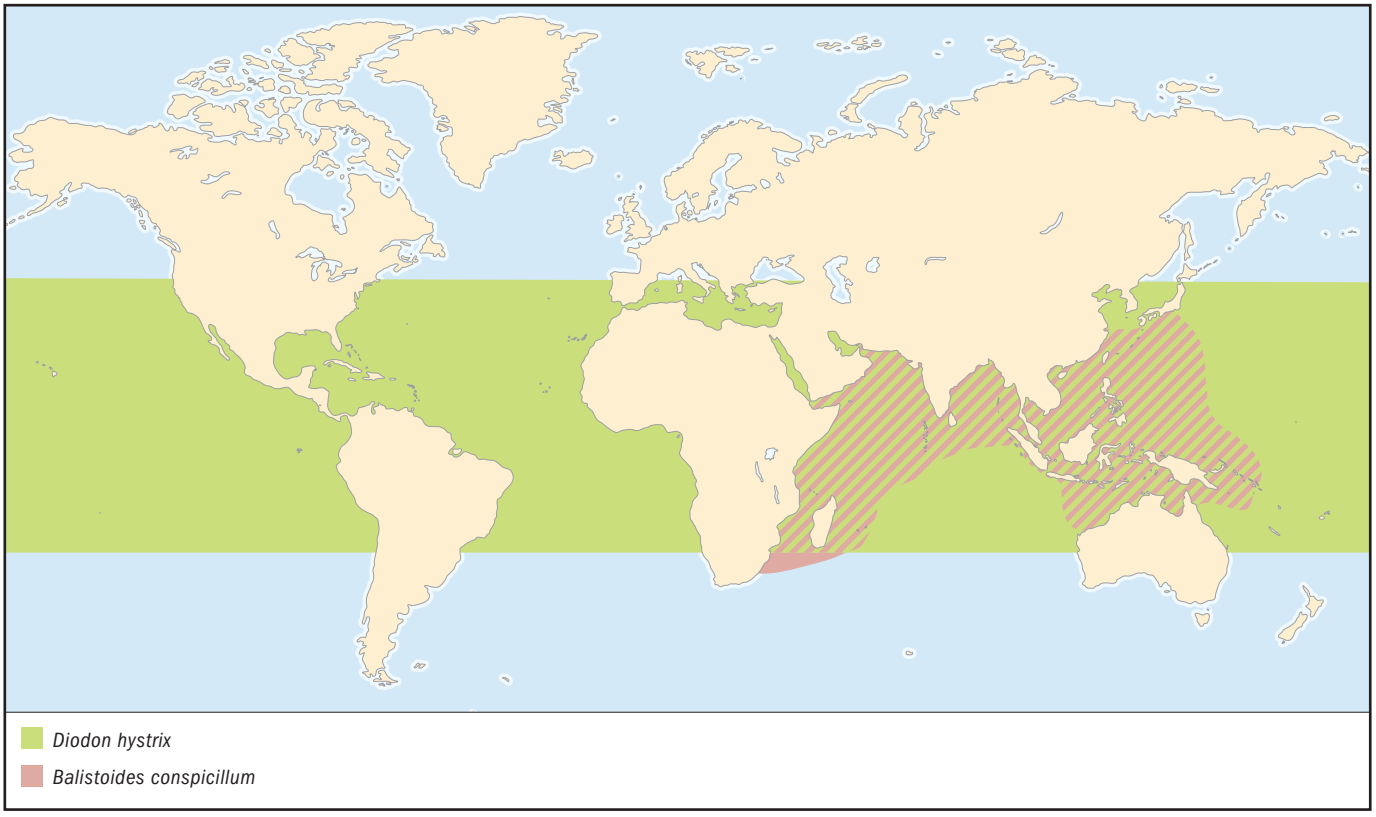
HABITAT
Occurs mainly on seaward reefs or passes along or adjacent to deep slopes or walls, from just below the surge zone to at least 246 ft (75 m).

BEHAVIOR
Generally solitary, territorial, and even aggressive.

FEEDING ECOLOGY AND DIET
Feeds upon benthic invertebrates, mainly crustaceans, including crabs, as well as sea urchins, mollusks, and tunicates.

REPRODUCTIVE BIOLOGY
Reproduction is consistent with that of others in the family, but greater detail is needed. Pair-spawns. Lays and defends demersal eggs in a nest. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN but relatively rare in many localities and may be vulnerable to overfishing.



SIGNIFICANCE TO HUMANS
A highly prized aquarium fish species, often collected as juveniles or subadults but occasionally full grown for larger aquaria. Also taken in subsistence and minor commercial food fisheries but has been implicated in ciguatera poisoning in humans. ◆

Blackbar triggerfish
Rhinecanthus aculeatus

FAMILY
Balistidae

TAXONOMY
Rhinecanthus aculeatus Linnaeus, 1758, India.

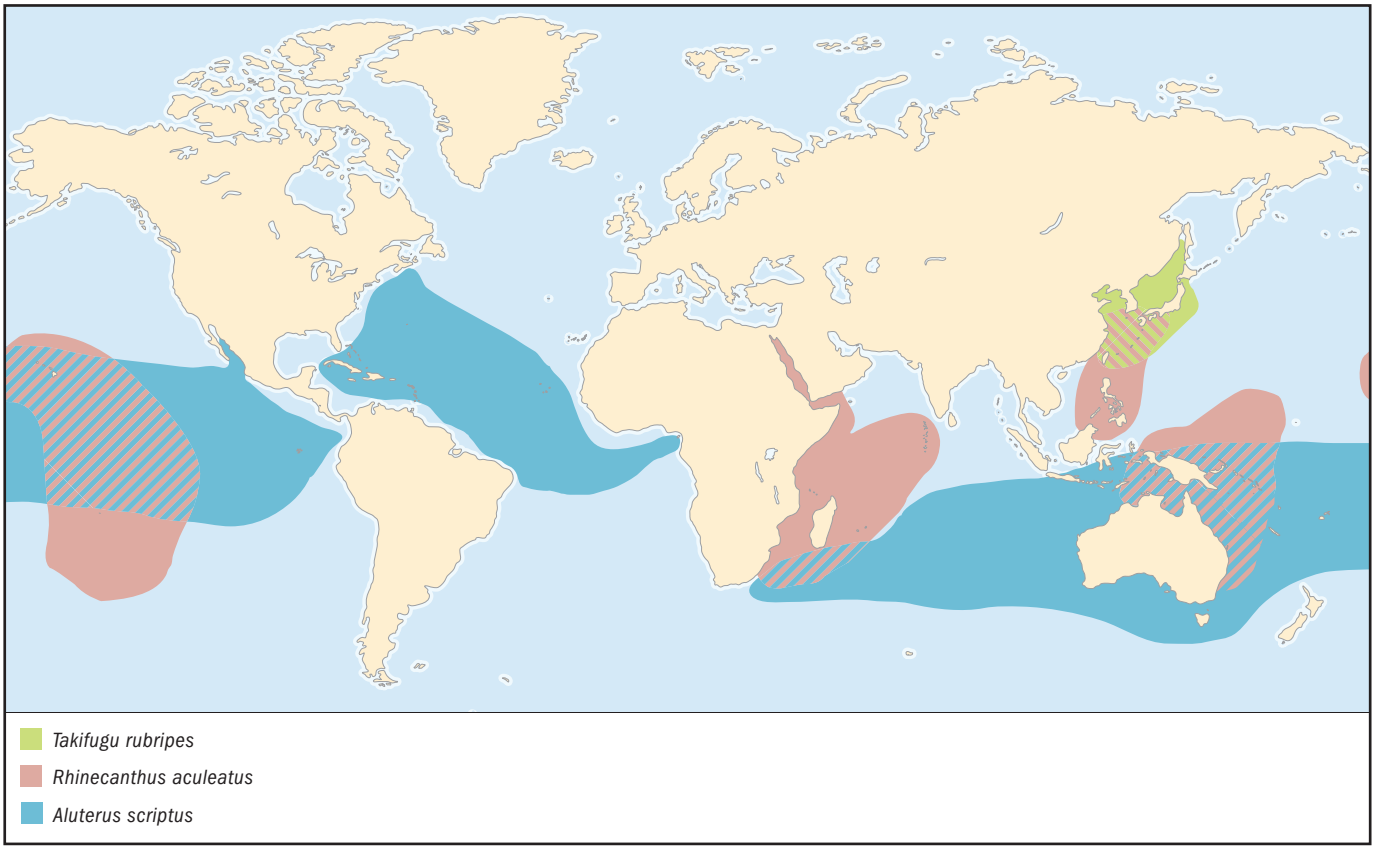
OTHER COMMON NAMES
English: Picassofish; English and Hawaiian: Humu humu; French: Poisson picasso sombre; German: Gemeiner Picassodrücker.

PHYSICAL CHARACTERISTICS
Body compressed and somewhat oblong or rhomboid. The forehead slopes upward past the eye to just anterior to the dorsal fin. There are three spines and 23–26 soft rays in the dorsal fin and 21–23 soft rays in the anal fin. The color pattern is gray to grayish brown on the head and just below the dorsal fin and brown to brownish gray along the upper flank, with two thick and two thin oblique stripes of the same color extending down, in alternation, onto the lower flank and belly. An orangish brown bar extends from midflank up and back to the base of the soft rays of the dorsal fin. The lower flank and belly are white. A thin yellowish line runs from the mouth back to just past the lower part of the operculum. There is a black to brown blotch extending from the posterior portion of the flank onto the white caudal peduncle and a black blotch around the anus. The fins are pale to light gray. Reaches 11.8 in (30 cm) in total length.

DISTRIBUTION
Tropical and subtropical Indo-West Pacific from the Red Sea and East Africa; south to South Africa; east to the Tuamotu Archipelago, Marquesas, and Hawaiian Islands in Polynesia; south to northern Australia and Lord Howe Island; and north to southern Japan. Also reported from the eastern Atlantic from Senegal south to South Africa.

HABITAT
Coral and rocky reefs, mainly on reef flats or in shallow lagoons on rubble and sand. Depth range is 3.3–13 ft (1–4 m).

BEHAVIOR
Highly territorial, especially when guarding a nest. Excavates or utilizes a small hole for shelter, where it can lock itself in by extending its first dorsal spine. It sleeps on its side there. Patrols a territory and may inflict a painful bite upon intruders or passersby. Produces a whirring sound when alarmed.



FEEDING ECOLOGY AND DIET
Omnivorous. Feeds upon mollusks, crustaceans, worms, sea urchins, corals, small fishes, tunicates, foramniferans, fish eggs, algae, and detritus.

REPRODUCTIVE BIOLOGY
The mating system is single male/multiple female polygyny, but facultative monogamy occurs occasionally. Spawning takes place on a semilunar cycle. Spawning is paired, and eggs are deposited on the substratum within a territory. The eggs are demersal and guarded. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An important fish in the aquarium trade but also taken as food in minor commercial and subsistence fisheries. ◆

Spot-fin porcupinefish
Diodon hystrix

FAMILY
Diodontidae

TAXONOMY
Diodon hystrix Linnaeus, 1758, India.

OTHER COMMON NAMES
English: Spot-fin porcupinefish; French: Diodon porc-épic; German: Gepunkter Igelfisch; Afrikaans: Penvis; Japanese: Nezumifugu.

PHYSICAL CHARACTERISTICS
Body elongate, stocky, and inflatable. Several long, strong spines cover the body, with a row of 20 stretching from the snout to the dorsal fin. The jaw has two fused teeth that are quite adept at crushing food items. There are 14–17 soft rays in the dorsal fin and 14–16 soft rays in the anal fin. The body color is grayish-tan, with small black spots and a white belly. A dusky-colored ring surrounds the belly. Grows to more than 35.4 in (90 cm) in total length.

DISTRIBUTION
Essentially circumglobal in tropical, subtropical, and warm temperate waters. From East Africa to San Diego, California, and Chile and the Galapagos Islands. Also in the Atlantic from Massachusetts and Bermuda to Brazil and from the Iberian Peninsula south to southern Africa.

HABITAT
Frequents coral and rocky reefs, usually in caves and holes to a depth of 164 ft (50 m). Swims in the water column during low-light periods.

BEHAVIOR
Generally solitary. Reportedly nocturnal but occasionally active in daylight.

FEEDING ECOLOGY AND DIET
Prefers hard-shelled benthic invertebrates that include gastropods, hermit crabs, and sea urchins.

REPRODUCTIVE BIOLOGY
Not well known, but paired courtship involving chasing has been observed just before sunset. Probably spawns demersal eggs. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN. May be vulnerable to overfishing, because it is normally not common anywhere.

SIGNIFICANCE TO HUMANS
Poisonous and not taken for food but collected and dried for use as ornaments. ◆

Mola
Mola mola

FAMILY
Molidae

TAXONOMY
Mola mola Linnaeus, 1758, Mediterranean Sea.

OTHER COMMON NAMES
English: Ocean sunfish.

PHYSICAL CHARACTERISTICS
Body large, tall, and compressed. The body is scaleless, with a thick, elastic skin. The mouth is small, with a parrot-like beak formed by fused teeth. The caudal fin is replaced by a clavus, a rudder-like body-fin adaptation. Both the dorsal and anal fins have relatively short bases but are very high. These fins are flapped in a synchronous motion that allows for reasonably good speed and also for swimming sideways. The pectoral fins are small and point upward toward the dorsal fin. There are 15–18 soft rays in the dorsal fin and 14–17 soft rays in the anal fin. The swim bladder is absent in adults. The color is silvery gray. The tips of the dorsal and anal fins and the clavus are darkly colored. Grows to more than 130 in (330 cm) in total length. Flesh may be toxic.

DISTRIBUTION
Circumglobal in tropical, subtropical, and warm temperate waters.

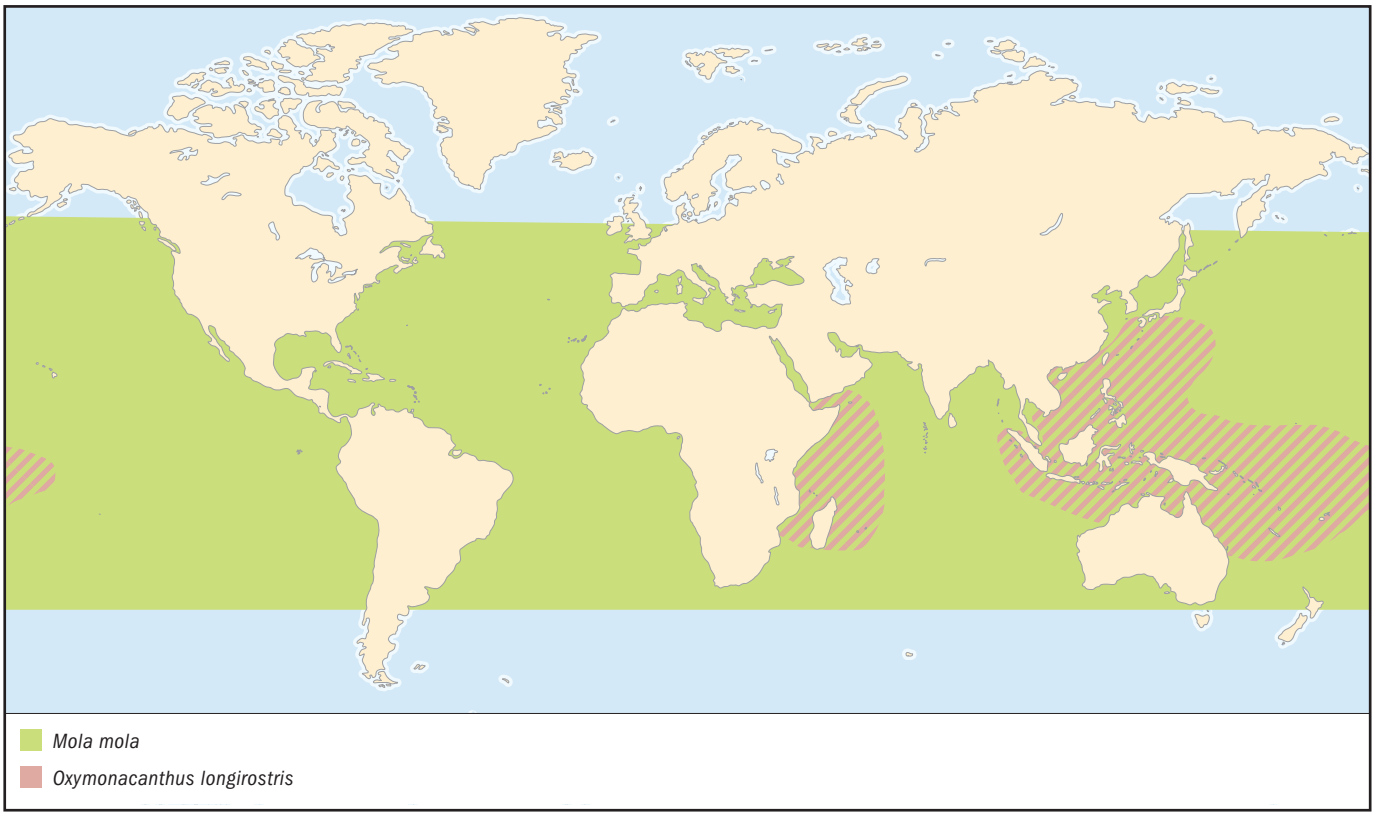
HABITAT
Frequents the pelagic realm but will move inshore to kelp beds. May be carried inshore by upwelling to the deep slopes of coral or rocky reefs. Depth range from surface down to 985 ft (300 m).

BEHAVIOR
Solitary but occasionally found in small groups. Swims up to the surface and even exposes its dorsal fin in the air. Also lies on its side.

FEEDING ECOLOGY AND DIET
Feeds on jellyfishes, larger zooplankton, crustaceans, and fishes; also takes mollusks and brittle stars inshore.

REPRODUCTIVE BIOLOGY
Not well known, but courtship probably is paired. Adult females are very fecund. Larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.



SIGNIFICANCE TO HUMANS
Prized as a delicacy in some places but avoided as poisonous elsewhere. Used in Chinese medicine. May be collected incidentally for large aquaria, but this species does not do well in captivity. ◆

Scrawled filefish
Aluterus scriptus

FAMILY
Monacanthidae

TAXONOMY
Aluterus scriptus Osbeck, 1765, China Sea.

OTHER COMMON NAMES
French: Robe de cuir; German: Schrift-Feilenfisch; Afrikaans: Bekrapte leerbaadjie; Japanese: Sôshihagi.

PHYSICAL CHARACTERISTICS
Body compressed, elongate, and somewhat rhomboid, with a concave snout and a relatively large and rounded caudal fin. There are two spines and 43–50 soft rays in the dorsal fin and 46–52 soft rays in the anal fin. The color is olive-brown to gray or tan with blue lines and spots in adults and yellowish brown with black spots in juveniles. Grows to more than 43.3 in (110 cm) in total length.

DISTRIBUTION
Tropical, subtropical, and warm temperate waters worldwide. In the Indo-Pacific from South Africa east to the Gulf of California and Colombia. In the Atlantic from Nova Scotia south to Brazil in the west and at Saint Paul's Rocks, Cape Verde, Ascension Island, and São Tomé Island in the east.

HABITAT
Found on seaward or lagoon coral reefs, rocky reefs, sea grass beds, and algae beds. Occasionally shelters under floating trees or other objects. Depth range is 13–394 ft (4–120 m).

BEHAVIOR
A solitary species that, despite its relatively large size, often moves cryptically within or between habitats.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds on hydrozoans, gorgonians, colonial anemones, tunicates, sea grass, or algae.

REPRODUCTIVE BIOLOGY
Not well known but probably lays demersal eggs. The larvae are pelagic and well equipped for a long pelagic existence, thus explaining this species' remarkable pattern of geographical distribution.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade. Also a game fish at some localities. Taken for subsistence elsewhere. This species has been reported to cause ciguatera poisoning. ◆

Longnose filefish
Oxymonacanthus longirostris

FAMILY
Monacanthidae

TAXONOMY
Oxymonacanthus longirostris Bloch and Schneider, 1801, East Indies.

OTHER COMMON NAMES
English: Harlequin filefish; French: Baliste à taches orange; German: Palettenstachier; Japanese: Tengukawahagi.

PHYSICAL CHARACTERISTICS
Body compressed and elongate with a pronounced, almost tubular snout. There are two spines and 31–35 soft rays in the dorsal fin and 29–32 soft rays in the anal fin. The color is bright green with orange spots or elongated blotches. The eyes are ringed with orange. The caudal fin is whitish with a small dark spot posteriorly. Grows to 4.7 in (12 cm) in total length.

DISTRIBUTION
Tropical and subtropical Indo-West Pacific from East Africa and Mozambique east to Samoa and Tonga, north to southern Japan, and south to the southern Great Barrier Reef and New Caledonia. The very similar congener *O. halli* replaces it in the Red Sea.

HABITAT
Found on coral-rich seaward and lagoon reefs, including reef flats, between 1.6 and 98 ft (0.5–30 m).

BEHAVIOR
Males and females most often are found in pairs that jointly patrol a shared territory. Territoriality is especially pronounced during mating season, and territorial defense is greater among males than females during this time, because females generally spend more time feeding. Aggressive behavior takes place in relation to food or mates. Males are capable of defending territories successfully alone during mating season, but females are not.

FEEDING ECOLOGY AND DIET
Feeds upon *Acropora* spp. coral polyps.

REPRODUCTIVE BIOLOGY
This species usually is monogamous but is facultatively polygynous in relation to the availability of mates locally. If males are in short supply, a male may have a two-female mating group. Eggs are demersal and laid almost daily during the season on a piece of filamentous algae, but no care is given. Algae that is toxic is preferred, because of the anti-predation advantage that it confers, in the absence of parental care, upon the eggs. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN but may be vulnerable because of coral bleaching.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade but does not do well without live coral. ◆

Longhorn cowfish
Lactoria cornuta

FAMILY
Ostraciidae

TAXONOMY
Lactoria cornuta Linnaeus, 1758, India.

OTHER COMMON NAMES
French: Coffre cornu; German: Langhorn-Kofferfisch; Afrikaans: Langhoring-koeivis; Japanese: Kôngo-fugu.

PHYSICAL CHARACTERISTICS
Boxlike body, with two long "horns" projecting forward from the top of the head just in front of the eyes. The mouth is subterminal with prominent lips. The dorsal fin is relatively small and arises just forward of the caudal peduncle. The caudal fin is rounded. There are eight or nine soft rays in the dorsal fin, eight to nine soft rays in the anal fin, and nine to 10 rays in the caudal fin. Body color ranges from green and olive to light orange with blue spots and is cryptic. Grows to at least 18.1 in (46 cm) in total length.

DISTRIBUTION
Indo-Pacific in tropical, subtropical, and warm temperate waters from East Africa and the Red Sea east to the Tuamotu Archipelago and the Marquesas in eastern Polynesia, north to southern Japan and southern Korea, and south to Australia and Lord Howe Island.

HABITAT
Coral and rocky reefs, especially in algae beds or sea grasses. Juveniles enter brackish waters of estuaries. Depth range is 3.3–328 ft (1–100 m).

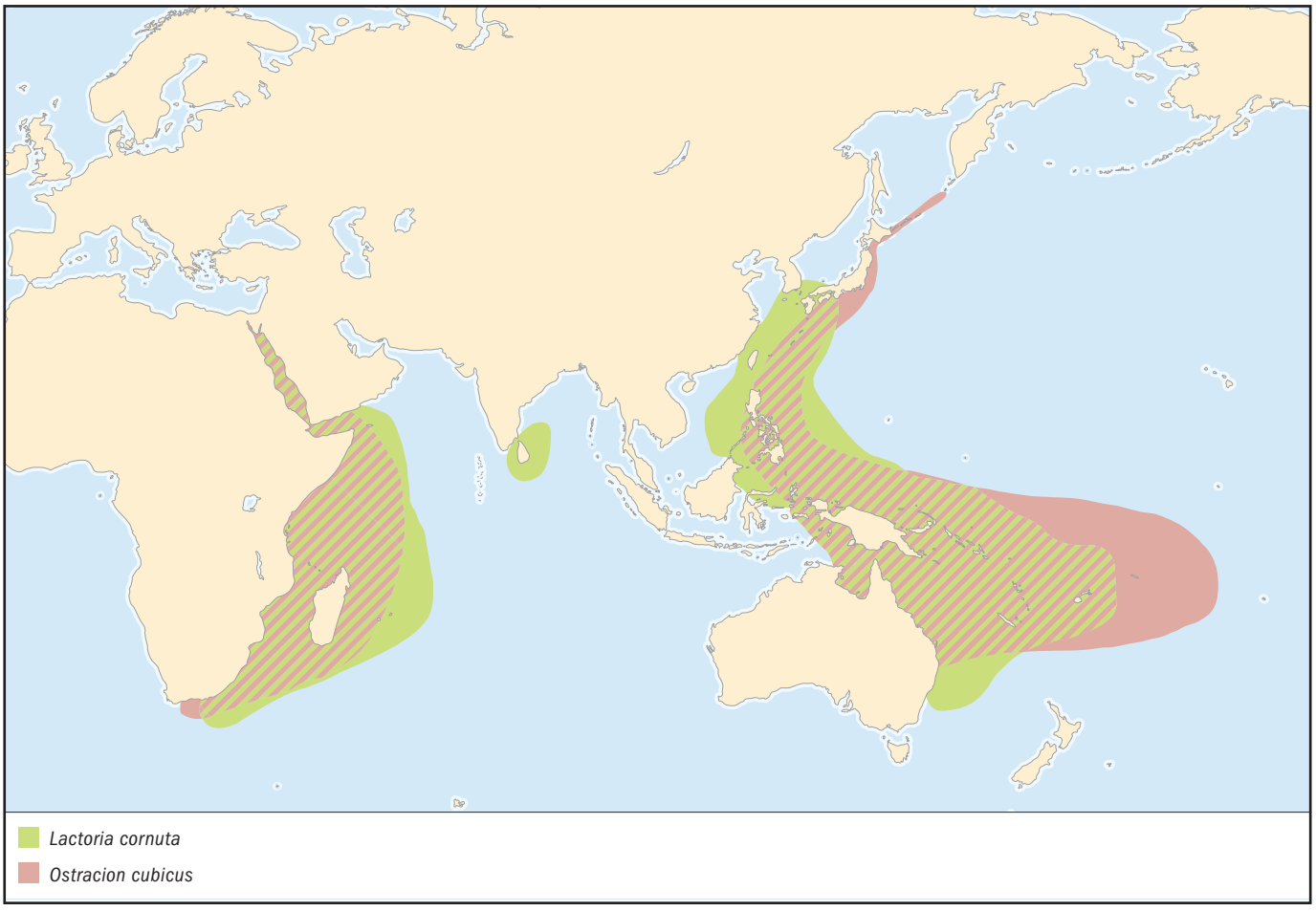
BEHAVIOR
Adults usually are solitary and territorial, but the juveniles form small groups.

FEEDING ECOLOGY AND DIET
Forages for benthic vertebrates by blowing water into the sand to dislodge them.

REPRODUCTIVE BIOLOGY
The mating system consists of a single male with a small group of females within its territory. Practices elaborate courtship just before or after sunset. Courtship is paired and results in the release of pelagic eggs well up into the water column above the bottom. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
An interesting aquarium species but one that should be kept alone or with species with which it is not likely to interact. Also taken as a minor subsistence species that may cause ciguatera poisoning. Most are probably dried and sold as ornaments. ◆



Yellow boxfish
Ostracion cubicus

FAMILY
Ostraciidae

TAXONOMY
Ostracion cubicus Linnaeus, 1758, India.

OTHER COMMON NAMES
French: Poisson cube; German: Gelbbrauner Kofferfisch; Afrikaans: Koffertije; Japanese: Minami-hakofugu.

PHYSICAL CHARACTERISTICS
Boxlike body with bony plates, a steeply sloping forehead, a subterminal mouth, a thick caudal peduncle, and a relatively large, somewhat rounded caudal fin. The dorsal and anal fins are positioned well back, just forward of the caudal peduncle. Body color of adults is a dirty yellow with a blueish hue and yellow seams between the body's bony plates. Juveniles are an attractive bright yellow with small black spots. There are eight or nine soft rays in the dorsal fin, nine soft rays in the anal fin, and 10 caudal fin rays. Total length up to 11 in (28 cm).

DISTRIBUTION
Tropical and subtropical waters of the Indo-Pacific and southeastern Atlantic, from East Africa and the Red Sea east to the Hawaiian Islands and the Tuamotu Archipelago in Polynesia, north to the Ryukyu Islands of southern Japan, south to Australia and Lord Howe Island, and off southern Africa in the Atlantic.

HABITAT
Primarily coral reefs in lagoons, on reef flats, and on protected seaward reefs. Juveniles associate with *Acropora* corals. Depth range is 3.3–148 ft (1–45 m).

BEHAVIOR
Adults are solitary and territorial. Juveniles also are solitary after settlement. Secretes ostracitoxin as a defensive mechanism when attacked or disturbed.

FEEDING ECOLOGY AND DIET
Omnivorous. Feeds upon benthic algae, various microorganisms, and foraminiferans that it strains from sediments, sponges, polychaete worms from sand flats, mollusks, small crustaceans, and small fishes. Large larvae and post-larvae often taken by pelagic predators, such as tunas.

REPRODUCTIVE BIOLOGY
Paired courtship just before or after sunset. Eggs and larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade but, due to its ability to secrete ostracitoxin, usually is a poor choice for a community aquarium. ◆

White-spotted puffer
Arothron hispidus

FAMILY
Tetraodontidae

TAXONOMY
Arothron hispidus Linnaeus, 1758, India.

OTHER COMMON NAMES
French: Tetrodon marbré; German: Weissflecken-Kugelfisch; Afrikaans: Witspikkel-blaasop; Japanese: Sazanamifugu.

PHYSICAL CHARACTERISTICS
Body elongate, robust, and capable of inflation with water. There are small spines on the body, except for the snout and caudal peduncle. The jaw teeth are fused but separated by a median suture. There are 10–11 soft rays in both the dorsal and anal fins. The caudal fin is rounded. Two fleshy tentacles emerge from each nostril. The gill opening is restricted, and the single lateral line is bent. The color is greenish brown with small white spots on the back, flanks, and caudal fin. The belly has white bars. Grows to at least 19.7 in (50 cm) in total length.

DISTRIBUTION
Tropical and subtropical waters of the Indo-Pacific from the Red Sea and East Africa to Panama and the Gulf of California; also north to Japan and throughout Micronesia and Polynesia as far as the Hawaiian Islands and Rapa Island and south to Australia and Lord Howe Island.

HABITAT
Coral and rocky reef slopes, lagoons, and inner reef flats over sand, rubble, or patch reefs. Juveniles found among weeds in estuaries or on reef flats. Depth range is 3.3–164 ft (1–50 m).

BEHAVIOR
Solitary and territorial. Individuals may bury themselves partially in the sand.

FEEDING ECOLOGY AND DIET
Omnivorous, feeding on fleshy coralline or calcareous algae, detritus, sponges, corals, anenomes, tube worms, mollusks, crabs, echinoderms, and tunicates.

REPRODUCTIVE BIOLOGY
Not well known. Probably lays demersal eggs. Larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade. ◆

Spotted toby
Canthigaster solandri

FAMILY
Tetraodontidae

TAXONOMY
Canthigaster solandri Richardson, 1845, Polynesia.

OTHER COMMON NAMES
English: Spotted sharpnose puffer.

PHYSICAL CHARACTERISTICS
Oblong and stocky body, with a pronounced snout, prickles on the belly, a rounded caudal fin, and the ability to inflate itself with water. Color is orangish red with blue spots over much of the body and on the orange caudal fin. The ventral surface is white. There is a black spot ringed in pale blue directly below the base of the dorsal fin. The dorsal fin is white, with a black base, and has eight to 10 soft rays. The anal fin also has eight to 10 soft rays. Some geographical variation in color pattern. The skin contains tetraotoxin. Grows to at least 4.3 in (11 cm) in total length.

DISTRIBUTION
Tropical and subtropical waters of the Indo-West Pacific from East Africa east to the Tuamotu Archipelago, south to the Great Barrier Reef and New Caledonia, and north to the Ryukyu Islands of southern Japan. Reportedly strays to the Hawaiian Islands.

HABITAT
Mainly coral reefs on reef flats, lagoon patch reefs, and seaward reefs. Depth range is 3.3–118 ft (1–36 m).

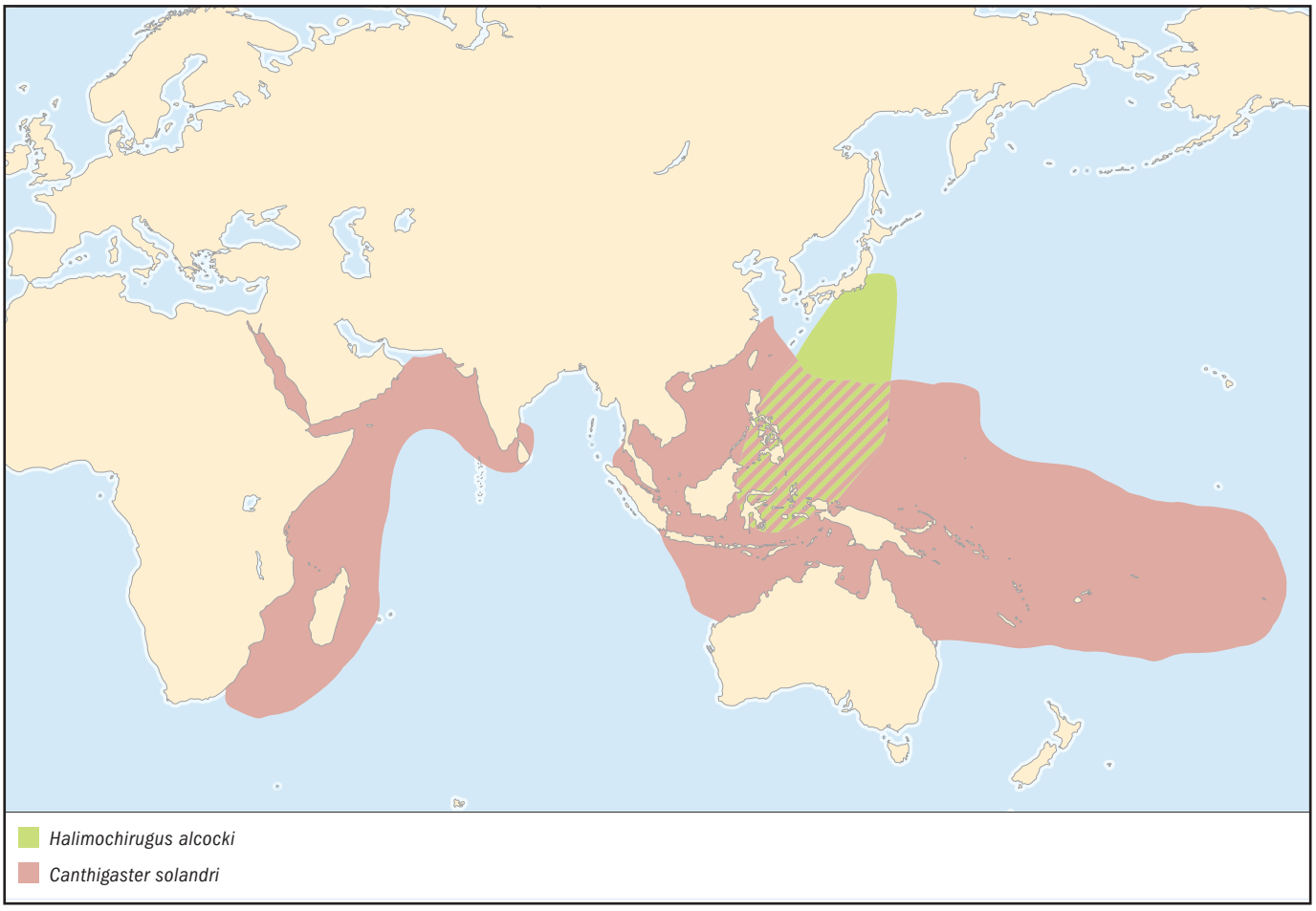
BEHAVIOR
Usually paired but also solitary or in groups. Swims over a home range, inspecting potential food items; also swims up in the water column. Some territorial interactions, as well.

FEEDING ECOLOGY AND DIET
Omnivorous, feeding on tunicates, bryozoans, echinoderms, crustaceans, mollusks, polychaete worms, corals, coralline red algae, green algae, and red algae.

REPRODUCTIVE BIOLOGY
Paired spawning of demersal eggs on algae growing on dead coral, rocks, or other substrata. The eggs are poisonous, and parental care is not practiced. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Collected for the aquarium trade. ◆



Fugu
Takifugu rubripes

FAMILY
Tetraodontidae

TAXONOMY
Takifugu rubripes Temminck and Schlegel, 1850, "Coasts of Japan."

OTHER COMMON NAMES
Japanese: Torafugu (tiger fugu).

PHYSICAL CHARACTERISTICS
Body oblong, compressed, and covered with prickles. Color is dark gray or grayish olive dorsally and white ventrally. A large black spot, ringed in white, is positioned on the flank just behind the pectoral fin. The dorsal fin has 16–19 soft rays, and the anal fin has 13–16 soft rays. The caudal fin is truncate. Poisonous, especially the ovaries, liver, and intestines. Grows to 27.6 in (70 cm) in total length.

DISTRIBUTION
Temperate waters of the northwest Pacific from the East China Sea and the Yellow Sea to the Sea of Japan as far north as Hokkaido.

HABITAT
Rocky reefs and shingle flats, usually up in the water column. Also frequents inlets and brackish waters but moves offshore with age and growth. Depth range is 3.3–656 ft (1–200 m).

BEHAVIOR
Solitary or in loose groups. This species swims about in the water column.

FEEDING ECOLOGY AND DIET
Omnivorous, feeding mainly on invertebrates.

REPRODUCTIVE BIOLOGY
The breeding season runs typically from March to May. Spawning is paired. Eggs are demersal and attached to rocks at depths of less than 65.6 in (20 m). Larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Highly prized in commercial fisheries of Japan. May be taken incidentally for aquaria. Also used in Chinese medicine. ◆

Spikefish
Halimochirugus alcocki

FAMILY
Triacanthodidae

TAXONOMY
Halimochirugus alcocki Weber, 1913, Arafura Sea.

OTHER COMMON NAMES
Japanese: Nagakawamuki.

PHYSICAL CHARACTERISTICS
Elongate body; the snout is tubular and elongate. There are six spines and 12–13 soft rays in the dorsal fin; the third spine is minute and protrudes through the skin, whereas the remaining spines lie beneath the skin. The anal fin has 11–12 soft rays. Grows to 6.7 in (17 cm) in total length.

DISTRIBUTION
Western Pacific from central Japan south to the Philippines and Indonesia.

HABITAT
A bottom-dwelling tropical and subtropical marine species at depths of 1,280–2,001 ft (390–610 m).

BEHAVIOR
Not well known.

FEEDING ECOLOGY AND DIET
Not well known but probably feeds on small benthic invertebrates that it takes with its tubelike snout.

REPRODUCTIVE BIOLOGY
Not well known but likely has demersal eggs and pelagic larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not significant as a food, sport, or aquarium species; of scientific interest, warranting further investigation. ◆

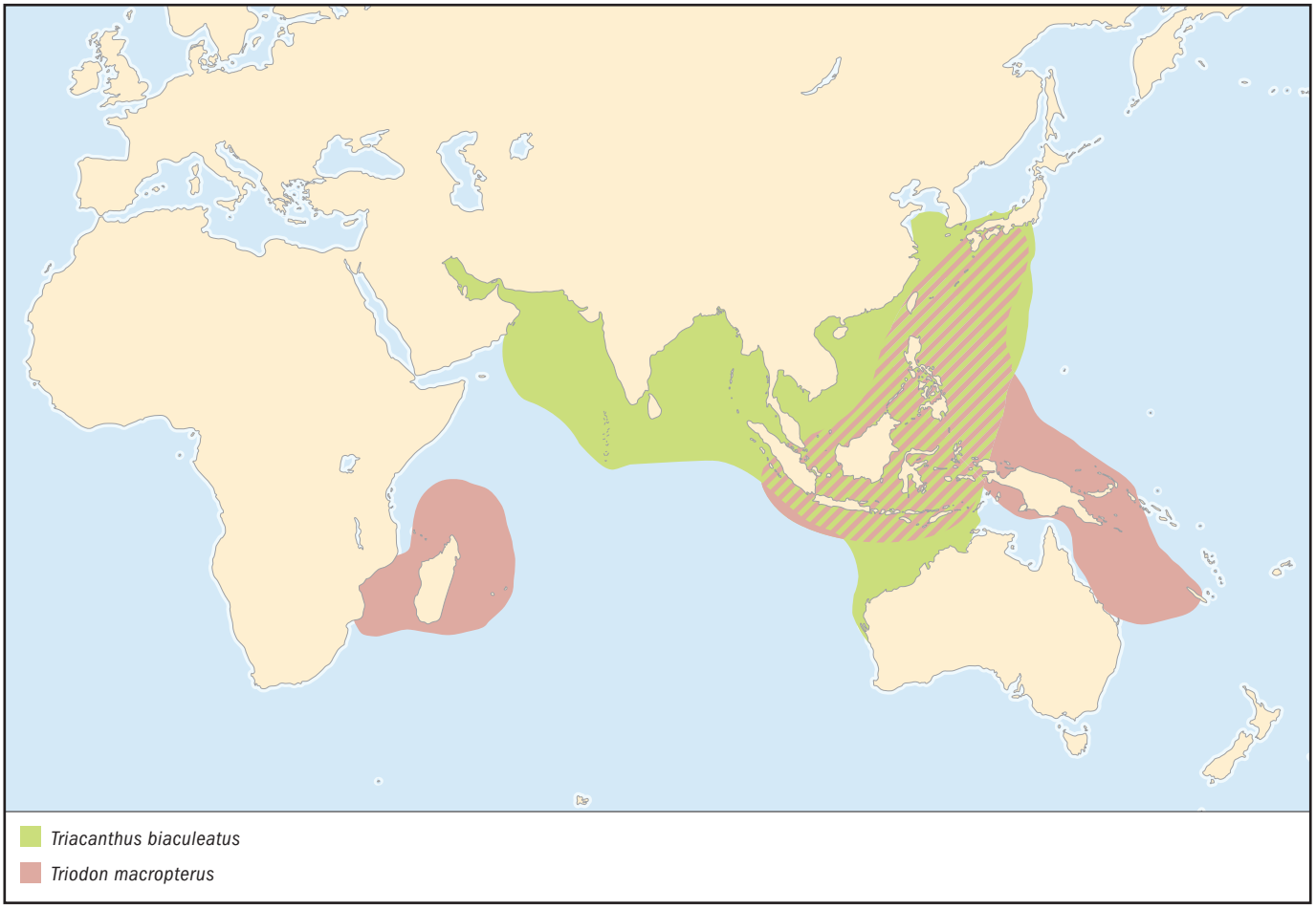
Triplespine
Triacanthus biaculeatus

FAMILY
Triacanthidae

TAXONOMY
Triacanthus biaculeatus Bloch, 1786, East Indies.

OTHER COMMON NAMES
English: Short-nosed tripodfish; Japanese: Gima.

PHYSICAL CHARACTERISTICS
Body oblong and compressed, with a long caudal peduncle, a deeply forked caudal fin with rounded lobes, a pronounced snout in the head, and a prominent dorsal spine. The dorsal fin has 20–26 soft rays, and the anal fin has 13–22 soft rays. Body color is silvery with a yellowish hue. The caudal fin is pale yellow and somewhat clear at the lobes. The fins are pale or milky to clear white, except for the dorsal spine, which is black at the base. Grows to at least 11.8 in (30 cm) in total length.



DISTRIBUTION
Indo-West Pacific region from the Persian Gulf east across the Indian Ocean to the east coast of Australia and north to China and southern Japan.

HABITAT
A shallow-water bottom-dwelling species in tropical and subtropical waters. Prefers sand or mudflats of estuaries and inshore coastal waters. Depth range to 197 ft (60 m).

BEHAVIOR
Not well known.

FEEDING ECOLOGY AND DIET
This species forages for benthic invertebrates.

REPRODUCTIVE BIOLOGY
Not well known but probably has demersal eggs, perhaps in a nest, with parental care. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
A minor commercial and subsistence species that also is used in Chinese medicine. ◆

Threetooth puffer
Triodon macropterus

FAMILY
Triodontidae

TAXONOMY
Triodon macropterus Lesson, 1831, Mauritius, Indian Ocean.

OTHER COMMON NAMES
Afrikaans: Drietand-blaasop; Japanese: Uchiwafugu.

PHYSICAL CHARACTERISTICS
Body oblong and compressed, with a well-developed ventral flap. The teeth are quite large and arranged in a beaklike plate; the lower teeth are completely fused, and the upper teeth are separated by a suture. Color is golden yellow with hints of white. There is an irregular black blotch, ringed in white, located medially at the base of the ventral flap. The dorsal and anal fins are relatively small and positioned posterior to the ventral flap. The dorsal fin has two spines and 10–12 soft rays, and the anal fin has nine to 10 soft rays. The caudal fin is slightly forked. Grows to 15.7 in (40 cm) in total length.

DISTRIBUTION
Tropical and subtropical waters of the Indo-Pacific from East Africa to Indonesia and the Philippines north to Japan and south to Australia and New Caledonia.

HABITAT
A deep-slope demersal species found above the bottom at depths of 164–984 ft (50–300 m).

BEHAVIOR
Not well known. Can inflate its body with water when threatened or attacked.

FEEDING ECOLOGY AND DIET
Not well known but probably feeds on benthic invertebrates.

REPRODUCTIVE BIOLOGY
Not well known. Probably lays demersal eggs. The larvae are pelagic.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
No commercial importance. May be taken incidentally for larger aquaria. ◆

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Organizations

IUCN/SSC Coral Reef Fishes Specialist Group. International Marinelife Alliance-University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96913 USA. Phone: (671) 735-2187. Fax: (671) 734-6767. E-mail: donaldsn@uog9.uog.edu Web site: <http://www.iucn.org/themes/ssc/sgs/sgs.htm>

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Glossary

Adipose fin—A small, fleshy fin without rays.

Afferent—Conducting impulses toward nerve centers or blood toward the gills. Compare efferent.

Agonistic behavior—Aggressive and submissive interaction between individuals of the same species.

Albinistic—Displaying the characteristics of an albino; an organism that has deficient pigmentation and white, colorless, or translucent skin and hair.

Amphidromous—Regular migration between fresh and seawater at different stages in their development.

Ampulla—A sac- or pouch-like anatomical swelling.

Anal fin—Fin located on the undersurface of the body, behind the anus.

Andropodium—Modified anal fin exhibited by some males.

Anoxic—Extreme deficiency of oxygen.

Anthropogenic—Caused by the activities of human beings.

Antitropical—Found in both Northern and Southern Hemispheres, but not in equatorial regions.

Aplacental—Without a placenta.

Axial skeleton—Skeleton of the main body and head.

Axillary process—Modified scale present at the upper or anterior base of the pectoral or ventral fins exhibited by some fishes.

Barbel—Fleshy, tactile projection resembling tentacles located near the mouth, chin, or snout.

Basiocapital—Bone located at the back of the head or skull; the occiput.

Basioccipital—Base of the head or skull.

Bathypelagic—Living and/or feeding in open waters at depths between 3,280 and 13,125 ft (1,000 and 4,000 m).

Benthic—Relating to, living on, or occurring at the bottom of a body of water.

Benthopelagic—Relating to, living on, or occurring on the bottom or midwaters of a body of water, feeding on benthic and free swimming organisms.

Benthos—The bottom of a body of water.

Bilobed—The division of matter into two lobes.

Branchial—Relating to the gills.

Branchiostegal membrane—The gill membrane; supported by the branchiostegal rays (bones).

Buccal cavity—Mouth cavity forward of the gills.

Bycatch—Species that are not targeted as catch, but are caught along with a target species during fishing.

Carapace—A hardened shell, such as turtles or crabs have.

Catadromous—Living in freshwater, but migrating to saltwater for spawning.

Caudal fin—Fin located at the end of the body, also known as the tail fin.

Caudal keels—Ridges on either side of the caudal peduncle that often function in stabilization during fast swimming.

Caudal peduncle—A narrow part of the body located at the base of the caudal fin.

Cavernicolous—Cave dwelling.

Cecum—Cavity or pouch extending off the intestine that receives undigested food.

Cephalic—Relating or belonging to the head.

Clade—A group of biological taxa, such as species, that includes all descendants of one common ancestor.

Cladist—One who classifies organisms based on their evolutionary history.

Cleithrum—The major bone of the pectoral girdle.

Cloaca—Chamber into which the intestinal, urinary, and reproductive ducts discharge.

Confluent fins—Fins that are joined or run together, having no true separation.

Crepuscular—Active in the twilight or evening.

Crypsis—Patterns and/or coloration that make an organism more difficult for predators to detect; protective patterns or coloration.

Ctenoid scales—Scales having minute spines on exposed surface.

Cupula—A cup-shaped structure.

Cycloid scales—Scales having smooth edges, absent of spines.

Demersal—Living near, laying on, or sinking towards the bottom of the ocean.

Dentary—Lower jawbone of vertebrates.

Dentine—Material similar to but harder than bone and is the principal mass of teeth.

Dermal denticles—Teeth-like scales, also known as placoid scales, on the skin of various elasmobranchs that acts as a protective barrier and also enables faster swimming.

Dextral—Occurring on or relating to the right side of the body.

Diadromous—Regular migration between freshwater and seawater.

Dichromatism—Partial color blindness; the ability to recognize only two colors.

Diel—Involving a 24 hour period of time; occurring on a daily basis.

Diploid—Two sets of chromosomes existing in a cell or organism.

Dorsal fin—Spined or rayed fin on the dorsal surface of body.

Dorsal—Relating or belonging to the back or top surface of the body.

Dorsolateral—Belonging to, or orientated between the dorsal and lateral surfaces.

Dorsoventral—Belonging to, or orientated between the dorsal and ventral surface.

Ectodermal—Formed from the outer germ layer of an embryo.

Ectothermic—Cold-blooded animal.

Efferent—Conducting impulses away from nerve centers or blood away from the gills. Compare afferent.

Elasmobrand—Relating to the group of fishes that includes the sharks, rays, and skates.

Electric organ—Organ capable of delivering an electric shock or used to emit electrical discharges to stun prey, repel predators, or detect objects.

Endemic—The restriction of a species to a particular geographic area or continent; native.

Engybenthic—Organisms living or occurring at the bottom of a body of water.

Epibenthic—Living on the bottom of the ocean.

Epigean—Organisms that are not cave-dwellers and do not live underground.

Epipelagic—Living or feeding in the uppermost layer of water; from the surface to midwater depths of 656.17 ft (200 m).

Euryhaline—Ability to live in waters of varying salinity.

Exogenous—Introduced from, or produced outside the organism or system.

Facultative parasite—An organism that can exist off of its host.

Falcate—Having a hooked or curved shape.

Filiform—Having the shape or form of a filament.

Fin base—Portion of a fin that attaches to the body.

Fin spine—Bony structure that supports the fin in more derived fishes.

Finlet—A small, isolated fin, usually without rays, that ususally occurs dorsally or ventrally on the caudal peduncle.

Flange—A rib or rim that aids one object in attaching to another.

Flexion—The act of bending, extending or flexing; a physical structure having a bent shape.

Fry—Newly hatched juveniles, or very small adult fishes.

Fusiform—The tapering of each end.

Ganglia—Mass of nerve tissue containing nerve cells external to the brain or spinal cord.

Ganoid—Relating to, or having scales that are made of bone and an outer layer that resembles enamel.

Ganione—Substance that resembles enamel and makes up the outer layer of certain fishes' scales.

Gas bladder—Sac in the body cavity below the vertebral column; helps maintain buoyancy, may aid in respiration, and may help produce or receive sound. Also called swim bladder.

Gill—Organ for obtaining oxygen from water.

Gill cover—Flap made of bone or cartilage that covers and protects the gills. Also called operculum.

Gill rakers—Projections from the gill arch that help in retaining food particles.

Globose—Having the shape or form of a globule or ball.

Gregarious—Living in a group or colony.

Haploid—One set of chromosomes existing in a cell or organism.

Hermaphroditism—The presence of both male and female sexual organs in one individual. When both organs occur at the same time, the individual is bisexual or a simultaneous hermaphrodita; if they occur at different times, the individual is a sequential hermaphrodite.

Heterocercal—Upper lobe of the tail is larger than the lower lobe, and the vertebral column extends into the upper lobe.

Heterozygous—Having two alleles at corresponding loci on homologous chromosomes that are different.

Holarctic—Relating to, or being from the northern parts of the world.

Homocercal—A caudal fin in which all of the principal rays attach to the last vertebra.

Homologous—Structures or properties of organisms shared through common ancestry.

Hyoid—Belonging or pertaining to the tongue.

Hypogean—Lives underground.

Hypoxia—Deficiency of oxygen reaching the tissues of the body.

Hypural plate—Modified last vertebra, to which caudal fin rays attach.

Incisiform—Teeth that are flat with sharp edges.

Integument—A layer or membrane that encloses or envelopes an organism or one of its parts.

Intertidal—Shallow areas along the shore that are alternately exposed and covered by the tides.

Isosmotic—Having the same osmotic pressure on two sides of a membrane.

Isthmus—Narrow, triangular area on the underside of the body, between the gill openings.

Iteroparous—Successive production of offspring, annually or seasonal batches.

Lacustrine—Relating to, inhabiting, formed or growing in lake water.

Lamella—Thin plate or membrane; often refers to smallest divisions of gill.

Larvaceans—Small transparent animals found in marine plankton; belong to subphylum Urochordata.

Lateral line—A series of ampulla forming a sensory organ to detect movements in water. Scales are often modified with pores opening to a sensory canal on the side of a fish.

Lecithotrophic—Embryos feeding on the yolk stored in the yolk sac.

Littoral—Related to, inhabiting, or situated near a shore.

Lunate—Having the shape of a crescent.

Maxilla—Upper jaw bone.

Median fin—Fins located on the median plane.

Meiobenthic—Benthic organisms with dimensions less than 0.02 in (0.5 mm) but greater than or equal to 0.004 in (0.1 mm).

Melanistic—An organism that exhibits a high amount of melanin (black coloration) in the skin.

Melanophore—A cell containing melanin.

Mesentary—A membrane that attaches organ to the abdominal wall.

Mesopelagic—Relating to, inhabiting or feeding at midwater at depths between 656.17 ft (200 m) and 3,280.84 ft (1,000 m).

Microphthalmic—Having eyes noticeably reduced in size.

Micropredator—A predator smaller than its prey that comes into contact with its host only when needing to feed.

Midwater—The middle stratum of a body of water.

Milt—The combination of spermatozoa and seminal fluid in fishes.

Monogamy—Mating system in which a single pair joins together for spawning and may remain together for one or more seasons.

Monophyletic—Developed from or related to a single common ancestral form or stock.

Monotypic—A group containing a single representative.

Myoglobin—Protein pigment in muscles that contains iron.

Naked—A fish that has no scales.

Nares—Nostrils.

Nasohypophysical—Nostril opening.

Nektonic—Organisms that swim strongly enough to move against currents.

Neural spine—The uppermost spine of a vertebra.

Notched fin—A fin that has patterned indentation.

Obligate air breathers—An organism that must receive a certain amount of their oxygen directly from air.

Ocelli—An eye-like marking.

Ontogenetic—Changes that incur from growth or age.

Oophagy—The process of embryos feeding on eggs produced by the ovary while still inside the uterus.

Osmoregulation—The regulation of water in the body.

Otoliths—Calcareous deposit in the ear capsules of bony fishes that show daily, seasonal or annual checks, rings or layers that can be used to determine ages.

Oviduct—Duct that serves as the passage of eggs from the ovary.

Oviparous—Production of eggs that develop and hatch outside of the mother.

Ovoviviparous—Fertilized eggs are retained in the mother's body during development.

Paedomorphic—Phylogenetic retention of larval or juvenile characters in the adult stage.

Paired Fins—Fins that occur in pairs, on each side of the body.

Paleoecology—The study of ecological characteristics in ancient environments and their relationships to ancient plants and animals.

Palp (Palpus)—Segmented and tactile process on the mouth.

PCBs (polychlorinated biphenyls)—Substances used as coolants and lubricants; their manufacture was banned in the United States in 1977.

Pectoral—Relating or belonging to the forward pair of appendicular appendages.

Pectoral fins—Fins attached to the shoulder or pectoral girdle, just behind the head.

Peduncule—Narrow part by which a larger part or the whole body is attached.

Pelagic—Relating to, living or occurring in open ocean water.

Pelvic fins—Pair of fins attached to the pelvis or pelvic girdle.

Photophore—A luminous spot or light-producing organ.

Piscivorous—Diet consists solely of other fishes.

Planktivorous—Diet consists solely of passively floating or weakly swimming animal and plant life.

Polyandry—Females mate with more than one male in a season.

Polygamy—Mating system in which individuals mate with more than one partner in a season.

Polygyny—Males mate with more than one female in a season.

Polyphyletic group—An assemblage consisting of different ancestral taxa, i.e., a group based upon convergence rather than on common ancestry.

Precaudal pit—Cavity just anterior to the caudal fin.

Prehensile—Adapted specifically to enable seizing, grasping, or wrapping around.

Promiscuity—Males and females spawn together with little or no mate choice.

Protandrous—Sequential hermaphroditism in which the fish functions first as a male and then a female.

Protrusible mouth—Mouth which can project forward and out to help catch prey.

Protygynous—Sequential hermaphroditism in which the fish functions first as a female and then a male.

Ray—Segmented bony rod or element that supports a fin membrane.

Riffle stretches—Areas of rough water caused by submerged rocks or a sandbar.

Rostral—Located toward the mouth or nasal region.

Seamount—Submarine mountain rising above the deep-sea floor.

Sexual dichromism—Exhibiting both male and female forms and aspects.

Sinistral—Occurring on or relating to the left side of the body.

Sinusoidal—Relating to, or shaped like the sine curve or wave.

Sister group—Closest relative to a taxa or group. The two groups share a common ancestor.

Spinules—Minute or miniature spine.

Standard length—Standard scientific measure of a fish's length; found by measuring from the most anterior part of the snout, lip or chin to the end of the last vertebra.

Subtidal—Zone just below the low-water mark of the tide that is never exposed, even at low tide.

Swim bladder—See Gas Bladder.

Syntopic—Sharing the same habitat within the same geographical range.

Tetraploid—Four sets (two homologous pairs) of chromosomes existing in a cell or organism.

Translocated—Transferred or dislocated specimens.

Tubercle—Nodule, growth, or knob present in an organ or on the skin.

Ventral—Relating to, or located in the abdomen or belly.

Vermicular—Relating to, caused by, or resembling worms.

Vestigial—Body part that was functional in ancestral sources but has become reduced or nonfunctional descendants.

Vitellogenesis—Deposition of yolk within the growing egg.

Viviparous—Producing live young.

Fishes family list

Myxini [Class]
Myxiniformes [Order]
Myxinidae [Family]

Cephalaspidomorphi [Class]
Petromyzoniformes [Order]
Petromyzonidae [Family]
Geotriidae
Mordaciidae

Chondrichthyes [Class]
Chimaerformes [Order]
Callorhinchidae [Family]
Chimaeridae
Rhinochimaeridae

Heterodontiformes [Order]
Heterodontidae [Family]

Orectolobiformes [Order]
Parascyllidae [Family]
Brachaeluridae
Orectolobidae
Hemiscyllidae
Ginglymostomatidae
Stegostomatidae
Rhincodontidae

Carcharhiniformes [Order]
Scyliorhinidae [Family]
Proscylliidae
Pseudotriakidae
Leptochariidae
Triakidae
Hemigaleidae
Carcharhinidae
Sphyrnidae

Lamniformes [Order]
Ondontaspididae [Family]
Mitsukurinidae
Pseudocarchariidae
Megachasmidae
Alopiidae
Cetorhinidae
Lamnidae

Hexanchiformes [Order]
Chlamydoselachidae [Family]
Hexanchidae

Squaliformes [Order]
Echinorhinidae [Family]
Dalatiidae
Centrophoridae
Squalidae
Etmopteridae
Somniosidae
Oxynotidae

Squatiniformes [Order]
Squatinidae [Family]

Pristiophoriformes [Order]
Pristiophoridae [Family]

Rajiformes [Order]
Pristidae [Family]
Torpedinidae
Narcinidae
Rhinidae
Rhinobatidae
Rajidae
Plesiobatidae
Hexatrygonidae
Dasyatidae
Urolophidae
Gymnuridae
Myliobatidae
Potamotrygonidae
Mobulidae
Urotrygonidae
Platyrhinidae
Zanobatidae
Narkidae
Hypridae
Rhinopteridae

Sarcopterygii [Class]
Coelacanthiformes [Order]
Latimeriidae [Family]

Ceratodontiformes [Order]
Ceratodontidae [Family]

Lepidosireniformes [Order]
Lepidosirenidae [Family]
Protopteridae

Actinopterygii [Class]
Polypteriformes [Order]
Polypteridae [Family]

Acipenseriformes [Order]
Acipenseridae [Family]
Polyodontidae

Lepisosteiformes [Order]
Lepisosteidae [Family]

Amiiformes [Order]
Amiidae [Family]

Osteoglossiformes [Order]
Osteoglossidae [Family]
Pantodontidae
Hiodontidae
Notopteridae
Mormyridae
Gymnarchidae

Elopiformes [Order]
Elopidae [Family]
Megalopidae

Albuliformes [Order]
Albulidae [Family]
Halosauridae
Notacanthidae

Anguilliformes [Order]
Anguillidae [Family]
Heterenchelyidae
Moringuidae
Chlopsidae
Myrocongridae
Muraenidae
Synaphobranchidae
Ophichthidae
Colocongridae
Derichthydae
Muraenesocidae

Nemichthydae
Congridae
Nettastomatidae
Serrivomeridae

Saccopharyngiformes [Order]
Cyematidae [Family]
Saccopharyngidae
Eurypharyngidae
Monognathidae

Clupeiformes [Order]
Denticipitidae [Family]
Engraulidae
Pristigasteridae
Chirocentridae
Clupeidae

Gonorynchiformes [Order]
Chanidae [Family]
Gonorynchidae
Kneriidae

Cypriniformes [Order]
Cyprinidae [Family]
Gyrinocheilidae
Catostomidae
Cobitidae
Balitoridae

Characiformes [Order]
Citharinidae [Family]
Hemiodontidae
Curimatidae
Anostomidae
Erythrinidae
Lebiasinidae
Ctenoluciidae
Hepsetidae
Gasteropelecidae
Characidae
Alestiidae

Siluriformes [Order]
Diplomystidae [Family]
Icaluridae
Bagridae
Claroteidae
Australoglanidae
Siluridae
Schilbeidae
Pangasiidae
Amphiliidae
Sisoridae
Amblycipitidae
Akysidae
Chacidae
Clariidae
Malapteruridae
Ariidae
Plotosidae
Mochokidae
Doradidae
Auchenipteridae
Pimelodidae
Cetopsidae
Aspredinidae
Trichomycteridae
Callichthyidae
Scoloplacidae
Loricariidae
Astroblepidae
Nematogenyidae
Heptapteridae
Pseudopimelodidae
Auchenoglanidae
Erthistidae
Claroglanididae

Gymnotiformes [Order]
Sternopygidae [Family]
Rhamphichthyidae
Hypopomidae
Apteronotidae
Gymnotidae

Esociformes [Order]
Esocidae [Family]

Osmeriformes [Order]
Argentinidae [Family]
Microstomatidae
Opisthoproctidae
Alepocephalidae
Platytroctidae
Osmeridae
Retropinnidae
Lepidogalaxiidae
Galaxiidae

Salmoniformes [Order]
Salmonidae [Family]

Stomiiformes [Order]
Gonostomatidae [Family]
Photichthyidae
Sternoptychidae
Stomiidae

Aulopiformes [Order]
Giganturidae [Family]
Aulopodidae
Synodontidae
Chlorophthalidae
Ipnopidae
Scopelarchidae
Notosuridae
Pseudotrichonotidae
Paralepididae
Anotopteridae
Evermannellidae
Omosudidae
Alepisauridae

Myctophiformes [Order]
Neoscopelidae [Family]
Myctophidae

Lampridiformes [Order]
Veliferidae [Family]
Lampididae
Stylephoridae
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A brief geologic history of animal life

A note about geologic time scales: A cursory look will reveal that the timing of various geological periods differs among textbooks. Is one right and the others wrong? Not necessarily. Scientists use different methods to estimate geological time—methods with a precision sometimes measured in tens of millions of years. There is, however, a general agreement on the magnitude and relative timing associated with modern time scales. The closer in geological time one comes to the present, the more accurate science can be—and sometimes the more disagreement there seems to be. The following account was compiled using the more widely accepted boundaries from a diverse selection of reputable scientific resources.

Geologic time scale

Era	Period	Epoch	Dates	Life forms
Proterozoic			2,500-544 mya*	First single-celled organisms, simple plants, and invertebrates (such as algae, amoebas, and jellyfish)
Paleozoic	Cambrian		544-490 mya	First crustaceans, mollusks, sponges, nautiloids, and annelids (worms)
	Ordovician		490-438 mya	Trilobites dominant. Also first fungi, jawless vertebrates, starfish, sea scorpions, and urchins
	Silurian		438-408 mya	First terrestrial plants, sharks, and bony fish
	Devonian		408-360 mya	First insects, arachnids (scorpions), and tetrapods
	Carboniferous	Mississippian	360-325 mya	Amphibians abundant. Also first spiders, land snails
		Pennsylvanian	325-286 mya	First reptiles and synapsids
	Permian		286-248 mya	Reptiles abundant. Extinction of trilobytes
Mesozoic	Triassic		248-205 mya	Diversification of reptiles: turtles, crocodiles, therapsids (mammal-like reptiles), first dinosaurs
	Jurassic		205-145 mya	Insects abundant, dinosaurs dominant in later stage. First mammals, lizards, frogs, and birds
	Cretaceous		145-65 mya	First snakes and modern fish. Extinction of dinosaurs, rise and fall of toothed birds
Cenozoic	Tertiary	Paleocene	65-55.5 mya	Diversification of mammals
		Eocene	55.5-33.7 mya	First horses, whales, and monkeys
		Oligocene	33.7-23.8 mya	Diversification of birds. First anthropoids (higher primates)
		Miocene	23.8-5.6 mya	First hominids
		Pliocene	5.6-1.8 mya	First australopithecines
	Quaternary	Pleistocene	1.8 mya-8,000 ya	Mammoths, mastodons, and Neanderthals
		Holocene	8,000 ya-present	First modern humans

*Millions of years ago (mya)

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